ANALYSIS OF Y-AXIS ORIENTATION IN AN INTERTIDAL CRAB, *Hemigrapsus nudus*

by

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ABSTRACT

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Many animals that live near shorelines (X-axes) perform horizontal movements perpendicular (Y-axes) to the nearest shore, which is referred to as Y-axis orientation (Ferguson and Landreth, 1966). Shore-directed (Y-axis) orientation was studied in the intertidal purple shore crab, *Hemigrapsus nudus*. The crabs were collected from several shorelines with different compass directions in southern British Columbia, Canada; i) in Barkley Sound, on the West Coast of Vancouver Island, ii) in the Nanaimo area on the east coast of Vancouver Island, and iii) in the Vancouver city area on the mainland coast. The directional preferences of the crabs were tested in orientation arenas. A seaward Y-axis orientation ability was established for crabs from the Vancouver Island shorelines. Vancouver city crabs showed a bimodal orientation parallel to the beach (X-axis orientation). Potential factors influencing Y-axis orientation were investigated. The directional preference and directivity of the orientation were not affected by the time of day, temperature, tidal cycles, level of activity, the moon, or the position of the observer. The crabs were presented with visual and non-visual orientation cues to determine the guiding mechanisms of the orientation. The results indicate that visual cues present in clear day and night skies are important for Y-axis orientation since high cloud cover and experimental interference with the natural sky visibility severely disrupted the orientation ability. Y-axis orientation based on non-visual cues was tested by subjecting crabs to altered magnetic fields. Results of these and other experiments suggest that non-visual cues may also be used in Y-axis orientation. Transplant experiments were conducted in which crabs from one area were relocated to a new beach with a different Y-axis. The directional preference in the seaward Y-axis direction of the original "home" beach persisted after 48 days on the new beach.

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I. GENERAL INTRODUCTION

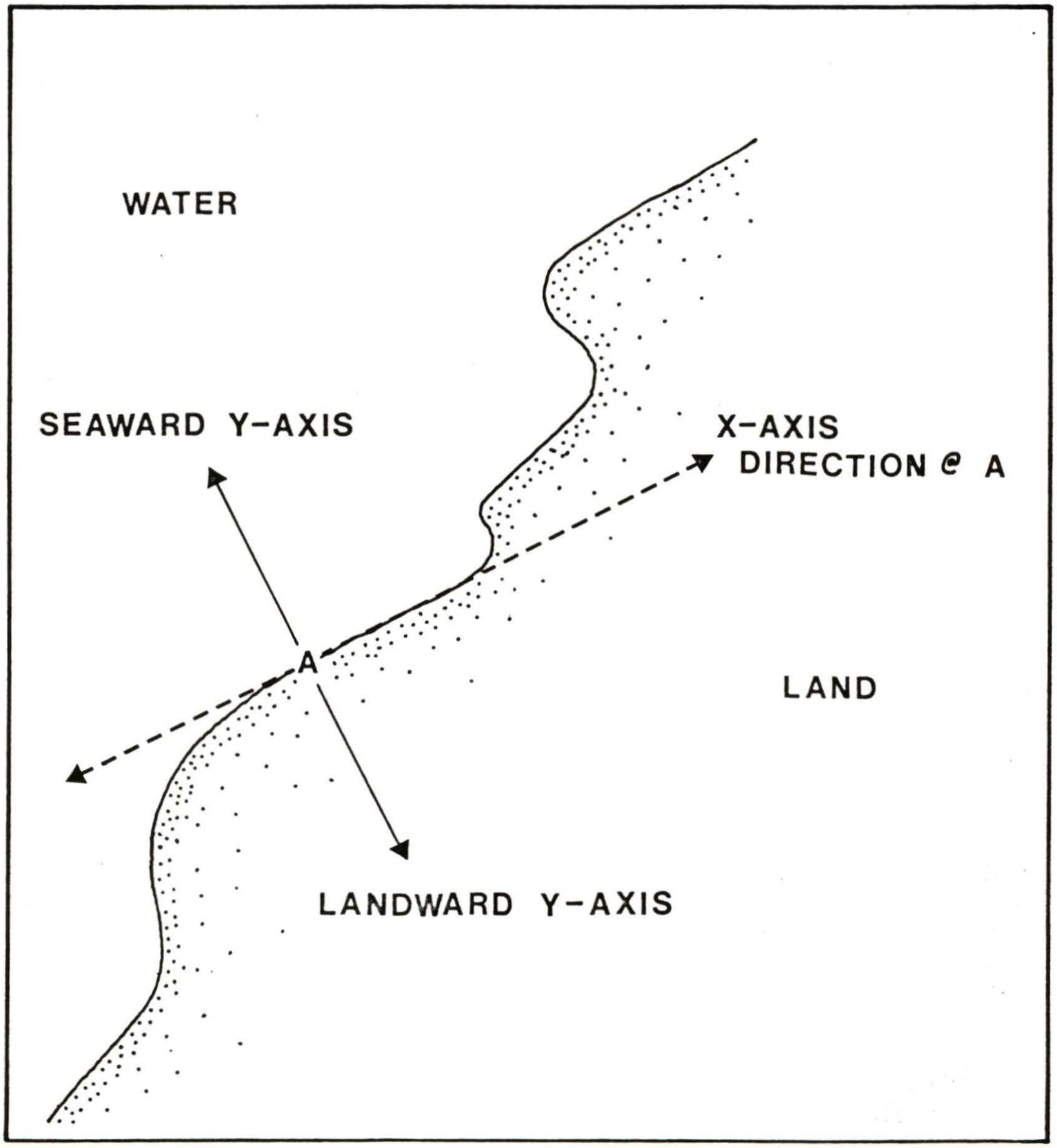
Many animals that live near shorelines (X-axes) perform horizontal movements perpendicular to the longshore axis (Y-axes), which is referred to as Y-axis orientation (Ferguson and Landreth, 1966) (fig. 1). The movements of shoreline animals exhibiting Y-axis orientation, such as amphibians and intertidal crustaceans, can be in either direction, i.e. seaward or landward. Y-axis orientation is a form of compass orientation, which may be defined as the ability of an organism to orient in a given compass direction without reference to landmarks when released in an unfamiliar territory (Able, 1980).

Different orientation cues used in direction finding during Y-axis orientation have been identified in various species. These cues include the sun, polarized light, moon, stars, and magnetism (for review see Herrnkind, 1972, 1983; Able, 1980, also next chapter).

Purple shore crabs, *Hemigrapsus nudus*, are small Grapsoid crabs up to 4 cm in body size. Their common color is mottled purple and green, with white spots on the claws (frontispiece). However, colors can range from completely white, green, purple, pink, orange, brown, or mottled combinations of all these shades.

H. nudus are commonly found in intertidal areas along the Pacific coast from Yakob Island, Alaska, to Turtle Bay, Mexico (Hart, 1982). In British Columbia, these crabs are most abundant on shores with medium to high surf action, where rocks and stones greater than about 15 cm in size cover a sandy or rocky substrate low in silt content. Here they may reach a density of up to $500/m^2$. These crabs can withstand relatively long periods of desiccation and are found along the whole breadth of the intertidal zone. They seldomly venture below the lowest low tide mark (Low, 1970). Their distribution on the beach is stratified, with the smallest individuals found in the high intertidal zone.

Figure 1. Explanatory diagram of X- and Y-axis directions. "A" is the point along the shoreline from which the crabs are collected.


WATER
SEAWARD Y-AXIS
X-AXIS
DIRECTION @ A
A
LAND
LANDWARD Y-AXIS

Intertidal crabs are subjected to environmental conditions and predation factors which vary predominantly in directions perpendicular to the shoreline. These include physical effects posed by the surge of the surf, such as removal of habitable substrate and the deposition of sediments. Displacement of the animals themselves during periods of rough seas is also possible. Physiological effects which are imposed on the crabs include osmotic imbalance, anoxia, prolonged aerial exposure at low tide, and a variety of other factors. Predation pressure from shore-dwelling birds such as gulls and crows is always present when the crabs are exposed.

Y-axis orientation is important, since it allows intertidal crabs displaced either landward or seaward to return to the optimal location in their intertidal habitat and is thus regarded as a basic ecological prerequisite for the animals' existence (Creutzberg, 1975). A crab disoriented in either time or space on a beach will likely perish (Herrnkind, 1972).

The objective of this study was to examine Y-axis orientation of various populations of H. nudus in southern British Columbia, concentrating on the four following questions:

1) Do populations of *H. nudus* from different geographical locations show Y-axis orientation?

2) What factors affect the orientation abilities of the crabs?

3) What sensory cue(s) are the crabs using to orient?

4) Are the crabs capable of learning a new orientation direction?

The organization of this report is as follows. Chapter II provides pertinent literature on Y-axis orientation in shore-dwelling inhabitants. Chapter III reviews the general materials, methods of testing, and data analyses used in the orientation research on *H.*

nudus. The results of this research are presented in 4 sections. Part 1 (Chapter IV) reveals the orientation response in various populations of H. nudus. Part 2 investigates the factors affecting the Y-axis orientation response in Chapters V and VI. Part 3 (Chapter VII) concentrates on determining which guiding cues the crabs are able to utilize in Y-axis orientation. Part 3 (Chapter VII) discusses the consequences of trying to alter the Y-axis orientation response by transplanting one population of crabs to a different shoreline. Finally, Chapter IX presents a general summary and discussion of the research results.

II. HISTORICAL REVIEW OF Y-AXIS ORIENTATION

Many animals living near the interface of land and water show directional movements perpendicular to the shoreline (Y-axis orientation, Ferguson and Landreth, 1966). These shoreline inhabitants can be roughly classified as primarily aquatic, intertidal, or terrestrial. Each of the forms shows Y-axis escape movements whose direction (landward or seaward) clearly shows adaptive significance and can often be predicted from the species, season, ecology, or stage in the life cycle of the animals.

The first rigorous study of Y-axis orientation was done by Floriano Papi, Leo Pardi, and their associates in Italy, on the orientation of various species of beach-dwelling amphipods such as Orchestia mediterranea (Pardi et al., 1958), Talitrus saltator (van den Bercken et al., 1967; Papi, 1955, 1960; Papi and Pardi, 1963; Pardi, 1957; Pardi and Grassi, 1955; Pardi and Scapini, 1983; Pardi et al., 1958), Talorchestia deshayesei (Pardi, 1957; Pardi and Grassi, 1955; Pardi et al., 1958), Talorchestia martensii (Ercolini, 1964), and also the isopod, Tylos latreillii (Pardi, 1954). Somewhat later Hamner et al. (1968) discovered Y-axis orientation in Tylos punctatus, the sand-beach isopod. The principal factor determining the directional preference along the Y-axis for these animals is humidity in the environment. When desiccated, these animals head seaward and when too moist they travel landward. In this manner, they stay within an area of the intertidal zone providing the optimum relative humidity.

Papi and Tongiorgi (1963) investigated landward Y-axis orientation in 3 species of shore-dwelling wolf spiders, Arctosa variana, A. cinerea, and A. perita. These spiders live on river banks or on sandy beaches. Although the spiders are relatively resistant to desiccation, they are prone to drowning. Upon finding themselves on the water, they rapidly skate on the surface and perform landward Y-axis orientation. A similar response was elicited by experimental manipulation in an orientation arena.

Y-axis orientation was also demonstrated in some molluscs such as the intertidal marsh periwinkle, Littorina irrorata (Hamilton, 1978). These gastropods oriented in a landward Y-axis direction when displaced from their high tide place of refuge on plant stems in the upper intertidal zone to lower regions devoid of vegetation, where they were open to predation by benthic predators.

Interestingly, some species of nearshore fish such as the starhead topminnow, Fundulus notti, have also been found to perform Y-axis movements (Goodyear, 1970). When the fish were tested aerially on a dry surface or underwater in orientation arenas, they oriented their jumping or swimming movements by means of a sun-compass in the appropriate directions that would have returned them to the land-water interface at the place of their capture. The mosquitofish, Gambusia affinis, is also a near-shore dwelling species. When tested underwater in orientation arenas, these fish oriented landward, also by means of a sun-compass (Goodyear and Ferguson, 1969).

Ferguson and his associates demonstrated Y-axis orientation in a host of amphibian species such as frogs; Southern cricket frog, Acris gryllus (Ferguson et al., 1965), chorus frog, Pseudacris triseriata (Landreth and Ferguson, 1966), tailed frog, Ascaphus truei (Landreth and Ferguson, 1967a), Northern cricket frog, Acris crepitans (Ferguson et al., 1967), leopard frog, Rana pipiens (Dole, 1972; Jordan et al., 1968), and bullfrog, Rana catesbeiana (Ferguson et al., 1968), toads; Fowler's toad, Bufo fowleri (Ferguson and Landreth, 1966), plains spadefoot toad, Scaphiopus bombifrons (Landreth and Christensen, 1971), oak toad, Bufo quercicus (Goodyear, 1971), and American toad, Bufo americanus (Adler and Taylor, 1981), and newts; rough-skinned newt, Taricha granulosa (Landreth and Ferguson, 1967b), and red spotted newt, Notopthalmus iridescens (Taylor and Auburn, 1978). It was discovered that while some species orient solely along one of the Y-axis directions (towards land or towards water), others would orient along both, depending on the life stage, species, and physiological or psychological state of the animals.

Y-axis orientation is also prevalent in decapod crabs living near shorelines. Subtidal crabs which live near shorelines show Y-axis movements primarily directed in an offshore direction, towards refuge in deeper water. For example, Y-axis orientation is performed by the benthic blue crab, Callinectes sapidus (Nishimoto and Herrnkind, 1978; 1982). These crabs invade the intertidal zone from deeper water during the rising tide to forage, and move offshore during the next ebb tide. Nishimoto and Herrnkind (1978) noted that one of the characteristic behavioral patterns displayed by blue crabs when disturbed in the intertidal zone, is a rapid Y-axis movement to deeper water. Blue crabs were found to use the slope of the substrate, direction of wave surge, and the sun as orientation cues guiding their offshore Y-axis escape movements (Nishimoto and Herrnkind, 1978; 1982).

Rudloe and Herrnkind (1980) performed orientation experiments with subtidal horseshoe crabs, Limulus polyphemus. Horseshoe crabs emerge from the sea to mate and lay eggs on sandy intertidal areas. When this species was tested in a wave tank, they exhibited an offshore Y-axis orientation in response to wave surge directions.

Intertidal crabs such as fiddler crabs (Uca sp.), ghost crabs (Ocypode sp.), and mangrove crabs (Goniopsis sp.) spend their post-metamorphosis life in the intertidal zone and seldom venture past its borders. These species may be considered ecological equivalents of H. nudus. Ghost crabs, Ocypode ceratopthalma, live on sandy beaches within or near the intertidal zone, where they construct burrows. Daumer et al. (1963) noted that when the crabs were startled when out of easy reach from their burrow, they often showed an escape response directly to the sea, or in the opposite direction to the dry sand above the intertidal zone where they quickly burrow out of sight.

Schöne and Braemer (1963) studied orientation in the mangrove crab, Goniopsis cruentata. These crabs live in mangrove swamps and are abundant on the roots and trunks of the trees, and on wet, muddy shores

(Rathbun, 1918). Crabs tested in orientation arenas performed landward Y-axis orientation in response to polarized light cues. The landward Y-axis movement is an appropriate orientation response for mangrove crabs displaced from the vicinity of mangrove trees, since this type of escape response in a natural situation would lead the crabs back to refuge among the trees.

Sand fiddler crabs, Uca pugilator, have a similar lifestyle to the ghost crabs and orient in a similar manner. They emerge from their burrows in the high intertidal or supratidal zone at ebb tide and forage seaward along the exposed intertidal zone to the waterline. Their burrows offer the primary source of refuge for these crabs and they return to them at high tide or when startled in close proximity to the holes. When the crabs are at a distance from their burrows and are disturbed, they will exhibit landward Y-axis escape movements which are not directed towards the burrows, but toward the vegetation above the intertidal zone. However, should a fiddler crab locate an empty burrow during its landward flight, it will seek refuge there. These Y-axis movements are apparently guided by sun, polarized light, beach gradient, and landmark orientation cues (Herrnkind 1966; 1967; 1968; Young and Ambrose, 1978).

The adaptive significance of a landward Y-axis orientation in fiddler crabs is clear, since taking a Y-axis escape route is indispensable for survival. Fiddler crabs displaced seaward face predation from predatory fish and larger crabs, as their locomotory and burrowing efficiency is markedly reduced under water (Herrnkind, 1968). I have also observed that strong wave action at the land-water interface makes landward return for the fiddler crabs very difficult. A landward escape route is clearly advantageous.

Supratidal crabs are also known to perform Y-axis movements. The terrestrial hermit crab, Coenobita rugosus, leads a terrestrial lifestyle along coastal regions, with adults only entering the water to spawn. Vannini and Chelazzi (1981) reported that when the crabs were tested in an orientation arena without a view of landmarks, they performed a seaward Y-axis orientation. When the crabs were released on a beach with both the sea and beach visible, they oriented along the landward Y-axis. This type of orientation along the Y-axis is clearly adaptive for these crabs. While deprived of view of the sea in the arena, the crabs responded as though they had been displaced landward from it, and thus attempted to return to a location near the water. Visual distance from water may serve as a reference for the spatial distribution of these crabs. Conversely, when the crabs were released on the beach, they headed landward to a suitable nearshore habitat.

Y-axis orientation is thus a common ability of intertidal inhabitants, although perhaps not in near-subtidal and supratidal animals. It is not suprising that species living near shorelines perform Y-axis orientation. Movement along the Y-axis provides the fastest and shortest route to a different level of the intertidal zone and knowledge of the direction of the shore is important for survival, since environmental and predation factors change primarily along the Y-axis.

H. nudus is an ecological equivalent of the intertidal crab species previously studied. In this study I planned to determine whether this species also shows a similar Y-axis orientation, and to identify the orientation cues which guide *H. nudus* in Y-axis orientation.

III. GENERAL METHODS AND MATERIALS

This general methods and materials section serves as an explanatory and reference section of methods and materials common to all of the tests. In addition, each section also contains specific information on methods and materials.

A. COLLECTION LOCATIONS

The criteria for selecting crab collection beaches were 1) the Y-axis direction of the beach 2) sufficient crab abundance, and 3) straightness of the shoreline. Only shorelines which had a change in the X-axis of less than 10° over a 100 m distance measured at high tide, were used as collection sites. The compass directions of the Y-axis of the collection shorelines were determined with a handheld compass (Silva Ranger 15TDCL, Silva Ltd., Willowdale, Ont.). The Y-axes in this paper refer to the offshore directions, and all directions are indicated as magnetic compass directions, unless otherwise stated.

B. CHOICE OF EXPERIMENTAL ANIMALS

Crabs were collected by hand from under rocks at low tide at different times during the diel cycle, without respect for their sex. Crabs used were limited to individuals greater than 1.00 cm in size to reduce handling stress and injury associated with using small individuals. Night collections were done with the help of a head-lamp. Crabs were transported to the test facilities in 2.5 gallon white plastic buckets, 28 cm in diameter and 22 cm deep. Approximately 30 crabs were placed in each bucket. Crabs were left in the collection buckets if they were tested within 1 h of capture. Storage of animals for longer periods prior to testing was done in various sized light blue fiberglass holding tanks, which were supplied with running sea water (10-12°C) at all times.

All animals were tested within 24 h of their capture, unless otherwise noted. Time held in captivity was held to a minimum because of the possibility of response loss over time. Herrnkind (1968, 1972) stated that directional preferences wane in 1-4 days in fiddler crabs (Uca sp.) held indoors or in barren containers. This is likely due to loss of entrainment of endogenous rhythms to celestial cues.

Crabs were transported in the collection buckets to the testing site. The lid was left off the bucket during testing, giving the crabs a view of the sky. The angle of view from the center of the bucket was 65°. Each individual was only tested once. The crabs were returned to the collection area of their native beach after completion of each test. Successive test crabs were not collected from areas of the beach previously sampled.

C. APPARATUS

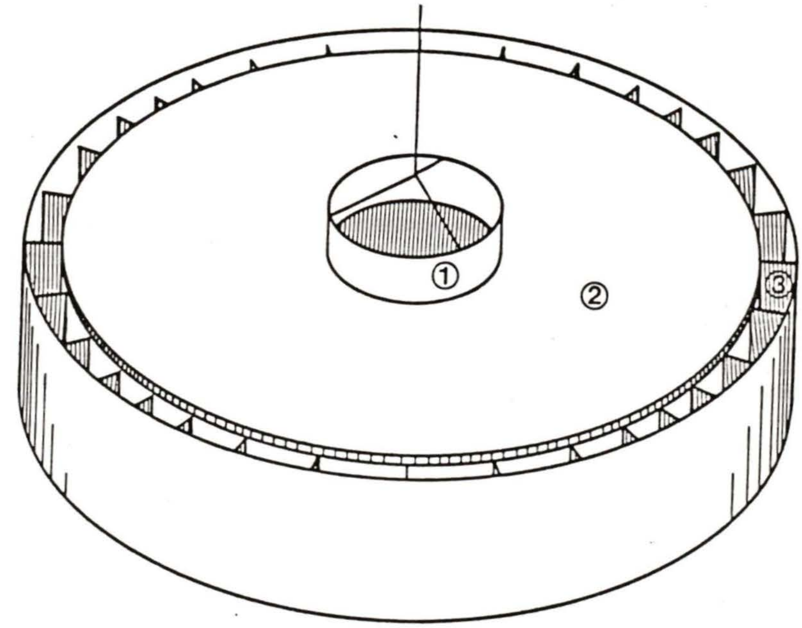
Two types of orientation arenas were used for testing the directional tendencies of the crabs.

1) Orientation arena #1 (fig. 2a) was constructed of stiff cardboard and painted flat black. A 79.0 cm diameter circular platform was centered in the 90.0 cm diameter arena. The edge of the platform was divided into 32 equally spaced pit traps. The apparatus rested on the ground while in use. The edge of the arena blocked off local landmarks, and gave a 157° angle of view from the center of the platform. At the onset of each trial, crabs were placed in a small cardboard release ring (20.0 cm diameter, 5.0 cm high) centered on the platform. The ring was then remotely raised via a thin string to release the crabs. To test crabs in complete darkness a lightproof cardboard lid, also painted flat black, was placed over the arena.

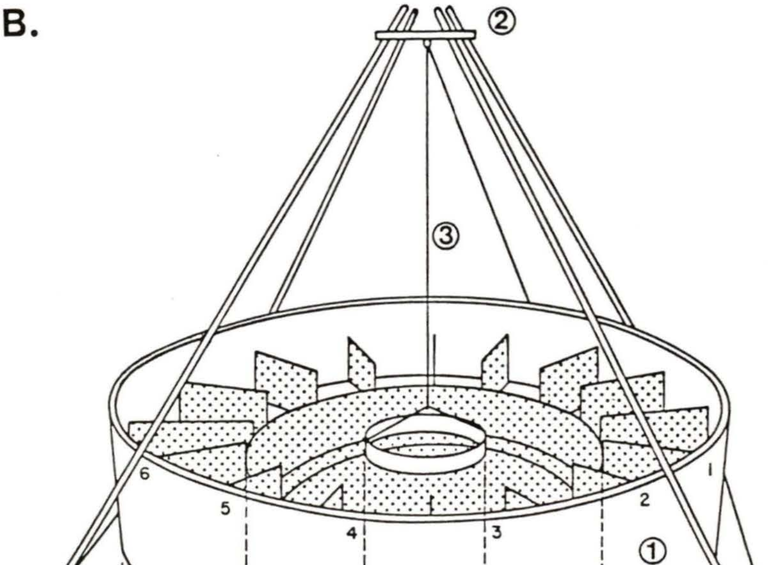
2) Orientation arena #2 (fig. 2b) consisted of a circular white plastic tank, 79.5 cm in diameter, with a clear, level platform of 50.0 cm

Figure 2. Orientation arenas. (a) freestanding arena #1 with 32 traps; (1) release ring, (2) platform, (3) traps, outside diameter of arena is 90.0 cm (b) arena #2 with 16 traps; (1) arena, (2) dowel supports, (3) release ring, (4) support table.

A.



B.



diameter centered inside. The space between the platform and the edge of the arena was divided into 16 black pit traps. Crabs were placed into a small black plastic release ring (16.0 cm diameter, 3.5 cm high) centered on the platform at the onset of each trial. The ring was raised remotely via a nylon thread to release the crabs. Four wooden dowels supported the raised ring. The angle of view from the center of the platform was 152°. Orientation arena #2 was supported by a wooden table with a hole in the middle of the table top of the same diameter as the platform of the arena. This hole allowed viewing of crabs from underneath the platform when necessary. A cover was placed over the hole to block the view when not needed for observation.

Non-magnetic metals were used in the construction of all apparatus to avoid possible interferrence with geomagnetic fields around the apparatus. Any apparatus specific to certain experiments is described in the appropriate sections.

D. EXPERIMENTAL PROCEDURE

The following outlines the general procedure common to all tests.

In the 1982 Bamfield tests, orientation arena #1 was used. For each experimental trial, groups of 20 crabs were randomly selected by hand from the collection bucket, and placed in the ring on the platform of the orientation arena. The crabs were held for 5 min and then released by lifting the ring, and were given 2 min to move. Any individuals remaining on the platform after 2 min were discarded and the crabs in the traps were counted.

For all other experiments, orientation arena #2 was used. Crabs were tested singly and were given 1 min in the ring and 1 min to make a trap choice early in the test series. These times were later changed to 30 s in the ring and 30 s to make a trap choice, when it became apparent that this was long enough for the crabs to quiesce. The mean time interval of crabs to make a trap choice was below 15 s, suggesting that the 30 s interval alloted for trap choice was of sufficient duration. Also, no appreciable decrease in the percentage of crabs making a trap choice was noted during the 30 s, as compared to a 1 min interval. Individuals were only tested once to ensure independence of data.

The arena and support table were independently and randomly rotated between trials in order to minimize effect of any anomalies present in the apparatus. The apparatus was levelled, which was critical since orientation to slopes as small as 1° has been found in some crustacean species such as the intertidal isopod, Tylos punctatus (Hamner et al., 1968). The blue crab, Callinectes sapidus, responds to slopes of 2° to 3° (Nishimoto and Herrnkind, 1978). The platform of the orientation arena was wiped in a circular motion after each release with a damp paper towel and then dried to eliminate or randomize possible directional odor cues left on the platform by previously tested crabs. The position of the observer and the direction of introduction of the crabs onto the platform were held constant for the duration of each test, but were randomly changed between tests.

Crabs on the platform were visually observed during the Bamfield 1982 tests and in the planetarium trials. In the Bamfield tests, the observer stood 4 m from the apparatus, and was visible to the crabs. No observer effect could be detected in the results. In the planetarium trials, the crabs were observed from underneath the apparatus through the clear plastic platform. Again, no observer effect on the orientation direction was evident.

In the tests performed with single crabs, it was evident that the animals were sensitive to the visual presence of the observer. During all of these and following tests the observer kept out of sight.

E. DATA RECORDING

i. Directional data:

The orientation arena was always lined up so that a randomly chosen trap had magnetic N at the center of that trap. Directional data consisted of recording the direction of the trap a crab fell into as a numerical value from 1-16. Each value corresponded to one of the 16 compass sectors (traps) of the orientation arena. In the 1984 tests, the time elapsed between release and trap choice was also noted. Animals that did not make a directional choice within the alloted time (30 s or 1 min) were removed from the platform and recorded as a "no choice". These crabs were not included in the directional analyses, but were used to determine the level of readiness to respond in some tests.

The sex and size of individuals were also recorded in some tests. The crabs in these experiments were first randomly tested without respect to sex or size, and then individually stored in compartmentalized plastic boxes for later sexing and measurement.

All times in this study are based on the 24 h clock, Pacific Standard Time (PST). Two handheld Silva Ranger 15TDCL magnetic compasses (Silva Ltd., Willowdale, Ont.) were standardized against each other and used in all of the experiments to determine compass directions.

ii. Other data:

For each test the following parameters were recorded:

1) origin of crabs, and date and time (PST) of capture
2) date, time (PST), and place of testing
3) arena trap at magnetic N (1-16)
4) height and flow direction of tide at test time

5) weather and wind direction (to nearest 45°) during test
6) % overcast = average % cloud cover of visible sky (sun was not obscured by overcast during daytime tests, unless otherwise specified). One hundred percent overcast represented a condition in which cloud cover obscured the whole sky, with no clear areas visible.
7) azimuth and elevation of sun or moon at start and end of test (to nearest degree)
8) temperature during test (to nearest degree)
9) compass direction of hidden experimenter (to nearest sector of arena)
10) compass direction from which crabs were introduced onto platform (to nearest sector of arena)

F. CALCULATIONS AND STATISTICAL ANALYSES

Because of the circular nature of the data, many calculations involved circular statistics. The following is a list of the analyses used.

1) Calculation of the mean direction (Batschelet, 1981): The mean direction of the unit vector (angle of travel) of the sample is α, where:

$$\begin{aligned} \alpha &= \text{arc tan } (S/C) \text{ if } C > 0 && (1)\\ &= 180° + \text{arc tan } (S/C) \text{ if } C < 0 \\ &= 90° \text{ if } C = 0 \text{ and } S > 0 \\ &= 270° \text{ if } C = 0 \text{ and } S < 0 \\ &= \text{undetermined if } C = 0 \text{ and } S = 0 \end{aligned}$$

and where: $S = \sum_{i=1}^{n} \sin \alpha_i$ and $C = \sum_{i=1}^{n} \cos \alpha_i$ (2)

α_i = directional angle of ith individual

n = sample size

This formula calculates the first-order vector, i.e. the vector resultant of a number of independent directions (Batschelet, 1981). It is important to note that the mean direction is only valid if the orientation is determined to be statistically significant ($p < .05$). In this study, however, mean directions are also presented for non-significant results, since even consistent non-significant mean bearings can be suggestive of orientation tendencies.

2a) Unimodal Rayleigh test (Batschelet, 1981)- tests whether the population from which the sample is drawn differs significantly from randomness, or, in other words, whether there is statistical evidence for one-sidedness or directedness (unimodality). The test statistic is "r", which is the mean vector length as defined by the formula:

$$R = \sqrt{\left[\left(\sum_{i=1}^{n} \cos \alpha_i\right)^2 + \left(\sum_{i=1}^{n} \sin \alpha_i\right)^2\right]} \qquad (3)$$

$$r = R/n \qquad (4)$$

where: n = sample size

α_i = directional angle of ith individual

R = length of resultant vector (Rayleigh's R)

2b) Bimodal version: tests for two-sidedness (bimodality) of the data. Animals often show bimodal choices in 180° opposite directions in orientation arenas. Analysis of such data involves doubling the angles of travel of each individual and reducing the multiples modulo 360°. The result is a unimodal sample and the new values may be used in the same formula as above. I assumed that the distribution is bimodal if the calculated r-value for the bimodal calculation was larger than for the unimodal one (Groot, 1965). If the angle between the two modes varies, no standard method is available to reduce the sample to a unimodal one (Batschelet, 1981).

The more concentrated the crabs are in a particular direction, the higher is the value of the mean vector length (r). The values can range from 0.0, which is randomness, to a high of 1.0, which signifies that all crabs travelled in exactly the same direction. In the case of bimodality, an r-value of 1.0 signifies that the animals showed equally strong orientation in 2 exactly opposed directions. Significance by the Rayleigh test indicates not only significant orientation, but also provides a measure of concentration of the observed directions about the mean direction(s).

The level of statistical significance in the Rayleigh test is strongly dependent on the sample size. The smaller the sample size, the higher the r-value has to be in order to achieve statistical significance of the mean orientation direction, which in this study was set at a probability of less than 5% ($p < .05$), unless otherwise stated. The critical values for all analyses in this research were obtained from tables found in Batschelet (1981), Rosner (1982), Snedecor and Cochran (1980), and Zar (1974, 1984).

3) Watson-Williams (two-sample and multisample) analysis (Zar, 1974)- The purpose of this test is to determine whether the mean bearings of several samples differ significantly from each other. The test compares the angular variance within the tests to the variance between tests. The "F" statistic is used, where:

$$F_{(k-1)(n-k)} = K\,[(n-k)\,(\sum_{j=1}^{k} R_j - R)]\,/\,[(k-1)\,(n-\sum_{j=1}^{k} R_j)] \qquad (5)$$

where: K = correction factor dependent on r (from tables)

n = sample size

k = number of samples compared

R_j = values of Rayleigh's R from the independent samples

R = values of Rayleigh's R calculated from the two samples being combined

The critical F-values and statistical significance are read from a table.

R-values can be derived from a unimodal or bimodal analysis of mean bearings. The results of the Watson-Williams analysis will significantly differ with the selection of R-values (ie. uni-, and bimodal R-values) for any one test. I used the largest R-values (those which most closely approximated the type of the circular distribution of the crabs) for the Watson-Williams analysis. However, the validity of using R-values other than unimodal ones has not been established in the literature. Multimodal Watson-Williams analyses have been judged here to be more representative of the true nature of the differences among tests, when used for analysing multimodal distributions.

When the Watson-Williams analysis is used on tests in which releases consisted of groups of crabs rather than individuals, the R_j and R values are calculated based on the weighed angles (see procedure under Hotelling's one-sample test). In this case, "n" represents the number of releases in a test, rather than the total number of crabs tested.

The Watson-Williams analysis is parametric with rather restrictive assumptions. One of these is that the sample is drawn from a von Mises (circular normal) distribution. Another assumption is that the r-value must be ~.75 or larger (Batschelet, 1981). Although this latter assumption was not attainable in my research this test was still favoured over the other, less powerful alternatives (Batschelet, 1981).

4) Hotelling's one-sample test (second-order analysis) (Batschelet, 1978) - Crabs tested in groups rather than singly can not be considered as independent data points (Batschelet, 1978; Childs and Buchler, 1982). In this case each release of a group of crabs was reduced to a single first-order vector by use of equation (1). The second-order vector was then derived from the group of first-order vectors to

determine whether the first-order vectors are significantly concentrated around some direction.

Before this analysis can be carried out, the first-order vectors have to be weighed with respect to the number of observations (group size) used in the determination of each vector. For example, group size varies with the number of crabs making a trap choice in group releases. The analysis is done by breaking down each first-order resultant vector into its weighed constituent sine and cosine components,
where:

$$x_i = S/n_i \qquad\qquad y_i = C/n_i \qquad\qquad (6)$$

n_i = number of observations (group size) for group i
x_i = weighed sin of mean vector for group i
y_i = weighed cos of mean vector for group i

$$S = \sum_{i=1}^{n} \sin \alpha_i \quad \text{and} \quad C = \sum_{i=1}^{n} \cos \alpha_i \qquad \text{(both from equation (2))}$$

The second-order mean vector (mean direction of travel of the entire group) is *, where;

$$\begin{aligned} * &= \text{arc tan } (y_i/x_i) \text{ if } x_i > 0 \qquad\qquad (7) \\ &= 180° + \text{arc tan } (y_i/x_i) \text{ if } x_i < 0 \\ &= 90° \text{ if } x_i = 0 \text{ and } y_i > 0 \\ &= 270° \text{ if } x_i = 0 \text{ and } y_i < 0 \\ &= \text{undetermined if } x_i = 0 \text{ and } y_i = 0 \end{aligned}$$

The second-order test statistic is F, where:

$$F_{(2)(N-2)} = \frac{(N-2)}{2(N-1)} \quad \frac{1}{1-(r)^2} \quad \left[(t_1)^2 - 2(rt_1t_2) + (t_2)^2)\right] \qquad (8)$$

and where: N = total number of groups

$$x = \left(\sum_{i=1}^{N} y_i\right)/N \qquad y = \left(\sum_{i=1}^{N} x_i\right)/N \qquad (9)$$

$$SS_x = \sum_{i=1}^{N} (x_i - x)^2 \qquad SS_y = \sum_{i=1}^{N} (y_i - y)^2 \qquad (10)$$

$$S_1 = \sqrt{[SS_x/(N-1)]} \qquad S_2 = \sqrt{[SS_y/(N-1)]} \qquad (11)$$

$$t_1 = (x/S_1)\ (\sqrt{N}) \qquad t_2 = (y/S_2)\ (\sqrt{N}) \qquad (12)$$

$$S_{xy} = \sum_{i=1}^{N} [(x_i - x)(y_i - y)] \qquad (13)$$

$$r = S_{xy}/[(N-1)S_1S_2] \qquad (14)$$

The restrictive assumptions of this test are that the sample must be drawn from a bivariate normal distribution and that the data are not grouped (Batschelet, 1978). In most of my tests, the sample did not seriously violate the first, but did violate the second assumption. However, this test still provided the best measure of other available tests.

5) The chi-squared test (Batschelet, 1981)- The purpose of this test is to determine whether the observed distribution fits one that is theoretically expected (in my tests a random distribution). This test was used to determine significant orientation in bimodal cases where the modes were not 180° apart. In cases such as these, the Rayleigh test is not powerful and may fail to reject randomness if in reality some type of bimodality or multimodality is present (Batschelet, 1981). This test was also used for other non-parametric analyses. To prepare the data for analysis, the circle with the data points is divided into a number of

equal sized arcs, so that each arc contains at least 4 data points (this assumption may not be violated). In each arc the number of data points is counted and compared to the expected frequency based on a random circular distribution. The test may be applied as in linear statistics with no adjustment to the circular case (Batschelet, 1981). The test statistic is X^2 where:

$$X^2 = \sum_{i=1}^{N} \left[(n_i - e_i)^2 / e_i \right] \qquad (15)$$

where: n_i = observed number of crabs in the ith given arc
e_i = expected number of crabs in the ith arc based on random orientation
N = number of arcs

The critical X^2-values (k-1 degrees of freedom) and statistical significance are read from a table.

6) Linear correlation- (Rosner, 1982) Standard linear correlation was used to determine significant linear relationships between various variables. Circular variables first had to be converted to linear data by various methods discussed in the appropriate sections where this test was used.

7) Test for a significant difference in concentration between 2 samples (r-value test) (Emlem and Penney, 1964; Batschelet, 1981) - The purpose of this test is to determine if 2 samples have significantly different concentrations (r-values) based on the resultant vector (R), irrespective of the mean bearings. The parameter of concentration used is k, where;

$$k = (n-1)/(2(n-R)) \qquad (16)$$

and R = length of resultant vector
n = sample size

The k-value is calculated for each of the 2 samples. The ratio of k_1/k_2 (the larger of the two k-values in the numerator) is calculated and compared to $F_{(n_1-1)(n_2-1)}$.

One assumption of the test is that the r-value of the 2 samples combined is larger than 0.70. Although this assumption was not attainable in my research, I still selected it since it was the only comparative measure of r-values available.

8) Bearing deviation test. The purpose of this test is to determine whether the mean bearing significantly differed from the expected direction. I know of no valid statistical method for circular analyses of this type. The V-test has been used in the past, however incorrectly (see Aneshansley and Larkin, 1981; Batschelet, 1981, p. 60).

A method was designed based on the well known Watson-Williams analysis (cf. 3 above). The mean bearing of the given distribution is compared to the expected direction for significant difference by creating a distribution of the sample points around the expected direction identical to that of the distribution to be compared. In essence, both distributions are equally concentrated (same r-values), and centered one about the mean bearing and the other about the expected direction. The Watson-Williams analysis is then performed as usual on the two distributions to detect statistically different bearings.

To perform the analysis, the sample distribution about the mean bearing is first converted to an identical distribution about a given expected direction, by the following method;

let; R_1 = length of the resultant vector of the original distribution (from section 2 above).

R_2 = length of the resultant vector of the new distribution about the expected direction.

In order for the orientation strengths to be equal between the two samples, let;

$$R_2 = R_1$$
$$\{\sin_2 = R_1 \ (\sin \alpha)$$
$$\{\cos_2 = R_1 \ (\cos \alpha)$$

where; α = expected bearing
$\{\sin_2$ = sum of sin of the new distribution
$\{\cos_2$ = sum of cos of the new distribution

These values are used in the Watson-Williams analysis for the expected distribution, which is compared to the original one. Significance of the analysis was considered as representing a significant deviation of the mean bearing from the expected direction.

After the test was developed, it was criticised on the grounds that the distribution of the test statistic cannot be the same as that of the Watson-Williams test statistic since the original and calculated sample distributions are not independent. The test was therefore eliminated from the analysis.

9) Confidence invervals (C.I.) - were the only available method to test whether the mean bearing (α) significantly differs from the expected direction (β). Confidence limits of $\alpha \pm \delta$ are first determined, where δ is the angle of deviation and is based on both the r-value and the sample size. If β lies outside the C.I., we conclude that the mean bearing differs significantly from the expected direction. 99% and 95% C.I.'s were used in this paper and were derived from C.I. charts in Batschelet (1981).

Part 1. Establishment of Y-axis orientation in H. nudus.

IV. Y-AXIS ORIENTATION EXPERIMENTS WITH VARIOUS POPULATIONS OF H. nudus.

INTRODUCTION

The objective of these experiments was to determine the extent and accuracy of Y-axis orientation in the purple shore crab, Hemigrapsus nudus, from several shorelines with different Y-axes in southern British Columbia, Canada; i) in Barkley Sound, on the West Coast of Vancouver Island, ii) in the Nanaimo area on the east coast of Vancouver Island, and iii) in the Vancouver city area on the mainland coast. Tests were performed in orientation arenas during the day and the night under 0-100% overcast skies.

A. BAMFIELD TESTS

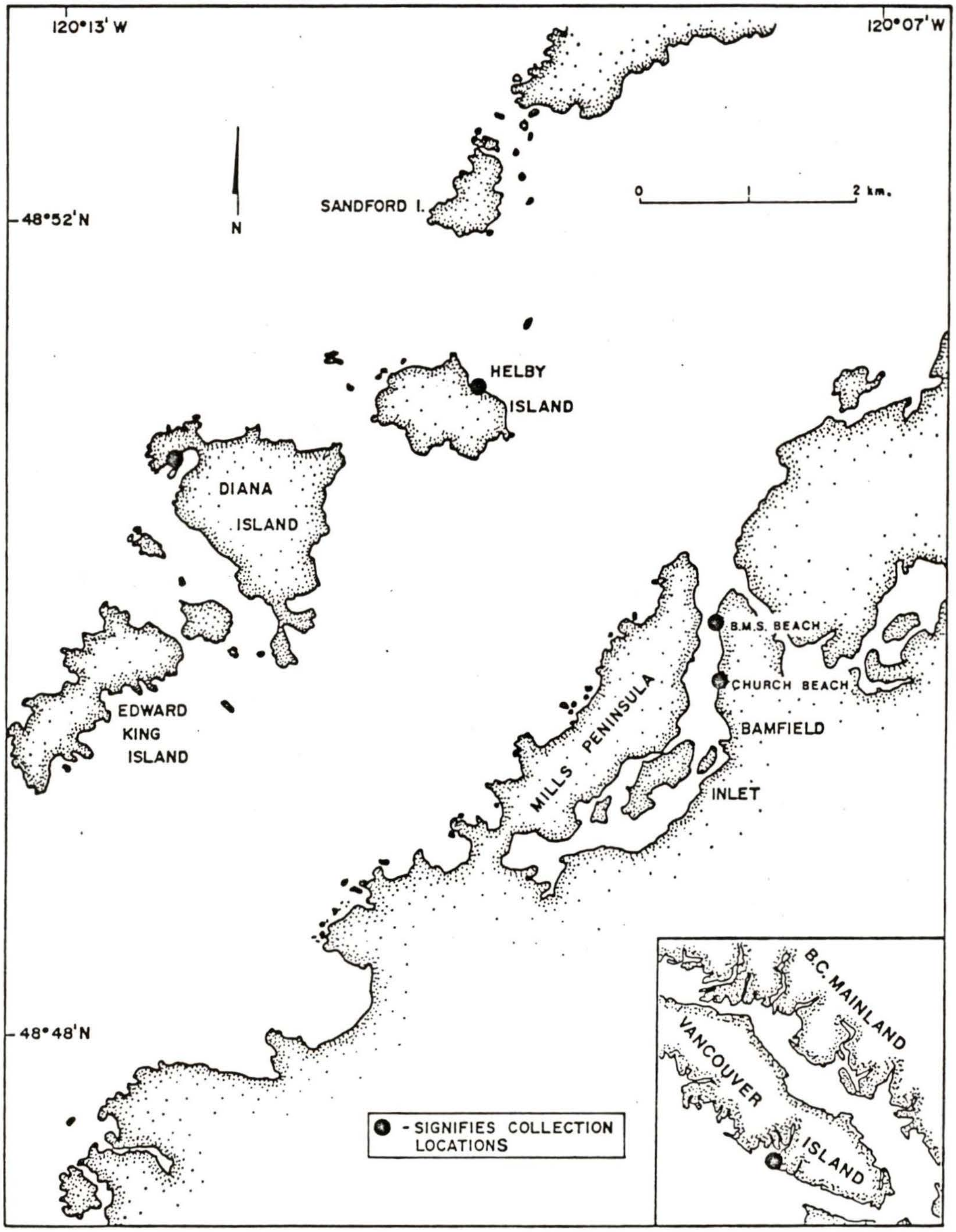
EXPERIMENTAL PROCEDURE

Crabs were collected from 3 shorelines in Barkley Sound, namely Bamfield Church beach (Y-axis = 305°N), Helby Island (Y-axis = 20°N), and Diana Island (Y-axis = 210°N) (fig. 3).

The Diana Island and Helby Island crabs were transported to the test facility by boat in open plastic buckets, while the Church beach stock was carried on foot. In the laboratory, crabs were held in barren light blue fiberglass trays (about 1 x 2 m and 30 cm deep) with running sea water and were tested within 24 h after capture.

Orientation arena #1 was used on the roof of the Cable Building at the Bamfield Marine Station. This building is isolated from the main laboratory and lies within 2 m of the shoreline. The testing area provided a good view of the sky in all directions, except in the N

Figure 3. Barkley Sound collection areas. Source: Canadian Hydrographic Service, Department of Fisheries and Oceans (D.F.O.), Ottawa, 1982.


120°13'W
120°07'W
48°52'N
48°48'N
N
SANDFORD I.
0
1
2 km.
HELBY ISLAND
DIANA ISLAND
EDWARD KING ISLAND
MILLS PENINSULA
B.M.S. BEACH
CHURCH BEACH
BAMFIELD
INLET
● - SIGNIFIES COLLECTION LOCATIONS
B.C. MAINLAND
VANCOUVER ISLAND

quadrant. A large hill and other buildings partially obstructed the view of the sky in this direction.

A total of 21 trials were performed during July 15-21, 1982. Crabs were tested in groups of about 20 and were given 5 min in the release ring and 2 min to make a trap choice after release. During the testing procedure, crabs were held in a shaded area in pans with sea water.

The mean bearing (first-order vector) and concentration around the mean direction were calculated for each release using the Rayleigh test (Batschelet, 1981), and the overall directional preference for the particular test condition (second-order vector) was then calculated from the first-order vectors using Hotteling's one-sample test (Batschelet, 1978).

RESULTS

The Bamfield tests were done under less than 20% overcast between 1130h - 1740h (table 1). All 3 populations showed statistically significant orientation (table 1, fig. 4). The Church beach crabs oriented in a mean bearing of 302°N, $p< .025$) (fig. 4a), the Helby Island crabs had a mean bearing of 21°N ($p< .001$) (fig. 4b), and the Diana Island stock had a mean bearing of 229°N ($p< .001$) (fig. 4c). These directions are similar to the seaward Y-axis directions for the 3 beaches, of 305°N, 20°N, and 210°N, respectively.

The results indicated that the crabs were not homing, since in that case the expected directions of travel from the Bamfield test area would have been 147°N toward Church beach, 290°N toward Helby Island, and 260°N toward Diana Island. It also follows from the results that land visible from the orientation arena to the N in the form of a prominent hill and buildings apparently had no effect on the orientation, since no bias in this direction was evident in the directional choices.

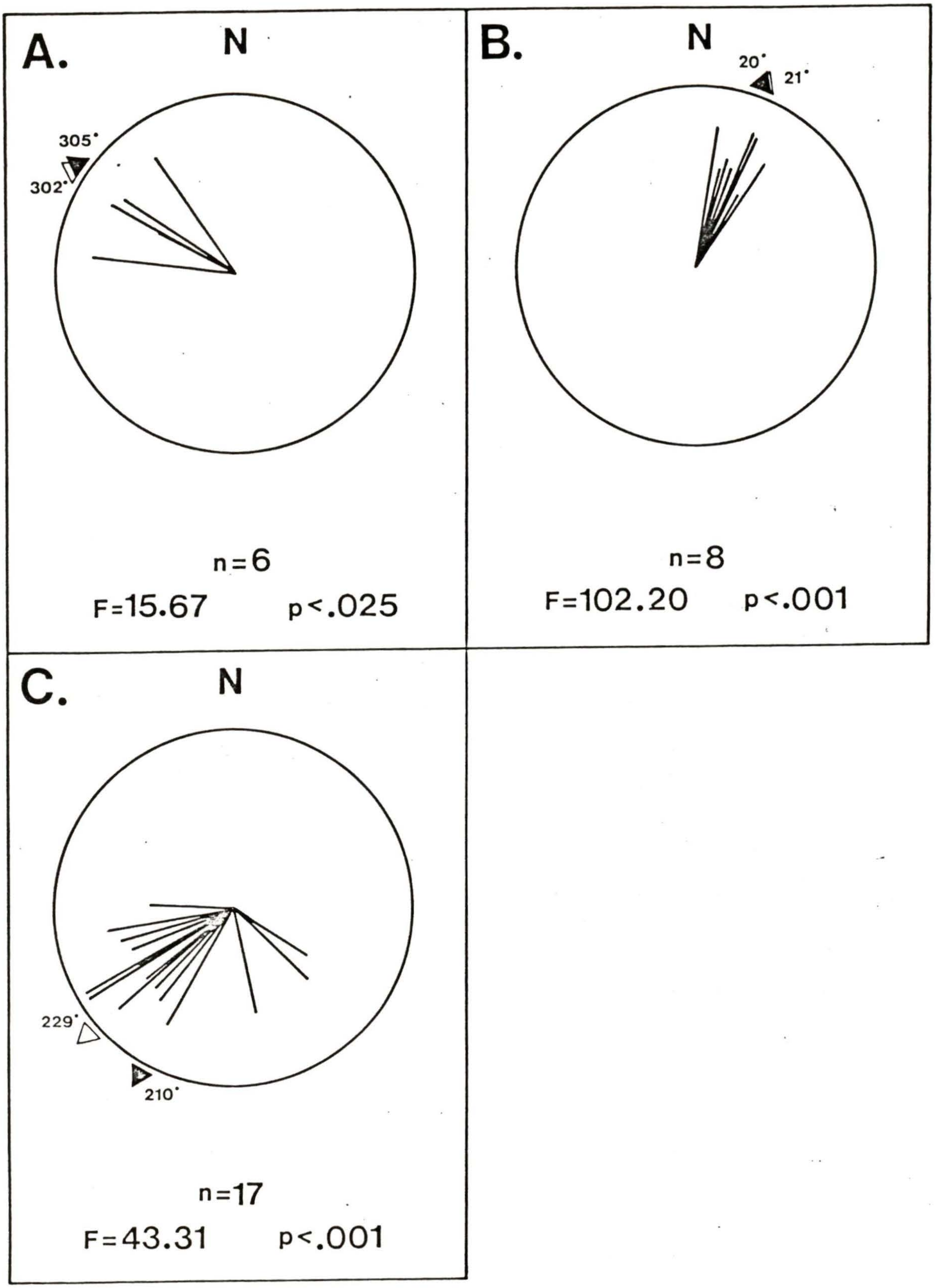
Table 1: Orientation of crabs from 3 beaches in the Bamfield area. Y-axes and mean bearings are in °N, F-value was derived from Hotelling's one-sample test (second-order analysis), and p = probability.

stock	% overcast	# of releases	# of crabs tested	Y-axis	mean bearing	F-value	p
Church beach	< 20%	6	115	305	302	15.67	< .025
Helby Island	< 20%	8	155	20	21	102.20	< .001
Diana Island	< 20%	17	323	210	229	43.31	< .001

Table 2: Results of daytime orientation tests with 3 Nanaimo crab populations. n = sample size, Y-axes and mean bearings are in °N, and p = probability.

test #	stock	% overcast	n	Y-axis	mean bearing	r-value	p
101	Rocky Point	0%	83	330	274	.50	< .001
103	P.B.S. beach	25%	109	150	126	.43	< .001
110	Piper's beach	50%	60	50	23	.56	< .001

Figure 4. Directional preferences of Barkley Sound crab populations; (a) Church beach (Y-axis = 305°N), (b) Helby Island (Y-axis = 20°N), and (c) Diana Island (Y-axis = 210°N), tested under a relatively clear daytime sky. Solid triangles indicate expected directions (seaward Y-axis), open triangles represent second-order mean bearings, bars indicate directional preference of each group of crabs released, length of bars represents the orientation strength (r-value) with the circle radius equal to unity, n = number of test groups. Significance levels are based on second-order analysis of unimodal angles.


A.
N
305°
302°
n=6
F=15.67
p<.025
B.
N
20°
21°
n=8
F=102.20
p<.001
C.
N
229°
210°
n=17
F=43.31
p<.001

From these results I conclude that H. nudus populations in the Barkley Sound area perform a seaward Y-axis orientation under experimental conditions when provided with a view of the clear day sky (< 20% overcast).

B. NANAIMO TESTS

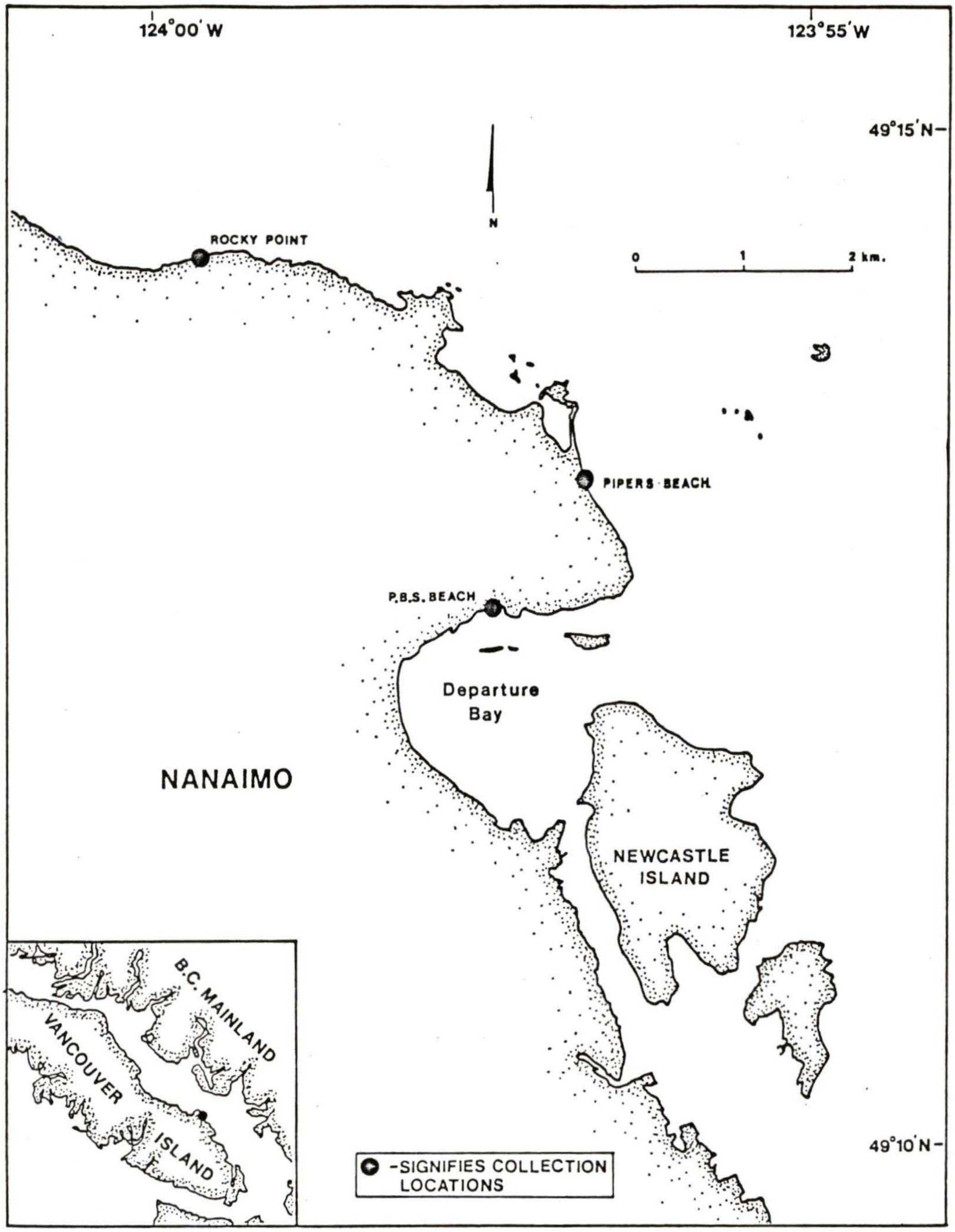
EXPERIMENTAL PROCEDURE

Crabs from 3 shorelines were tested; Rocky Point beach (Y-axis = 330°N), Piper's beach (Y-axis = 50°N), and Pacific Biological Station (P.B.S.) beach (Y-axis = 150°N) (fig. 5). The Rocky Point and Piper's beach stocks were transported to the testing facility by car in the collecting buckets with lids, while the P.B.S. stock was carried on foot in open buckets. Crabs were stored for less than 8 h prior to testing in barren fiberglass tanks (about 93 cm diameter and 75 cm deep) painted light blue, with running sea water. During testing, crabs were kept in open buckets and allowed a view of the sky.

Orientation arena #2 and the support table were used. Crabs were tested singly and given 30 s in the ring and 30 s to make a trap choice after release. All of these and following experiments were performed at the Pacific Biological Station, on the roof of the Clemens Building. The roof of this building was flat and was situated approximately 100 m from the ocean.

Daytime and nighttime tests were conducted under 0-70% overcast skies. For night tests, small 3 V flashlights with a double layer of plastic red filters (each layer >99% spectrally opaque in the 485-560 nm range and >84% between 300-485 nm) were used to locate the animals in the traps and to record data. H. nudus have a peak spectral sensitivity at 350 and 500 nm (Jordan and Kimeldorf, 1971) and thus the red filters significantly muted the light in the crabs' sensitive regions of visible and near-UV light. No other light source was used.

Figure 5. Nanaimo collection locations. Source: Canadian Hydrographic Service, D.F.O., Ottawa, 1983.


124°00' W
123°55' W
49°15' N
49°10' N
N
0
1
2 km.
ROCKY POINT
PIPERS BEACH
P.B.S. BEACH
Departure Bay
NANAIMO
NEWCASTLE ISLAND
B.C. MAINLAND
VANCOUVER ISLAND
● -SIGNIFIES COLLECTION LOCATIONS

The 3 initial experiments also served to determine the best sample size to be used in successive testing and the possible effect of crab sex and size on orientation.

RESULTS

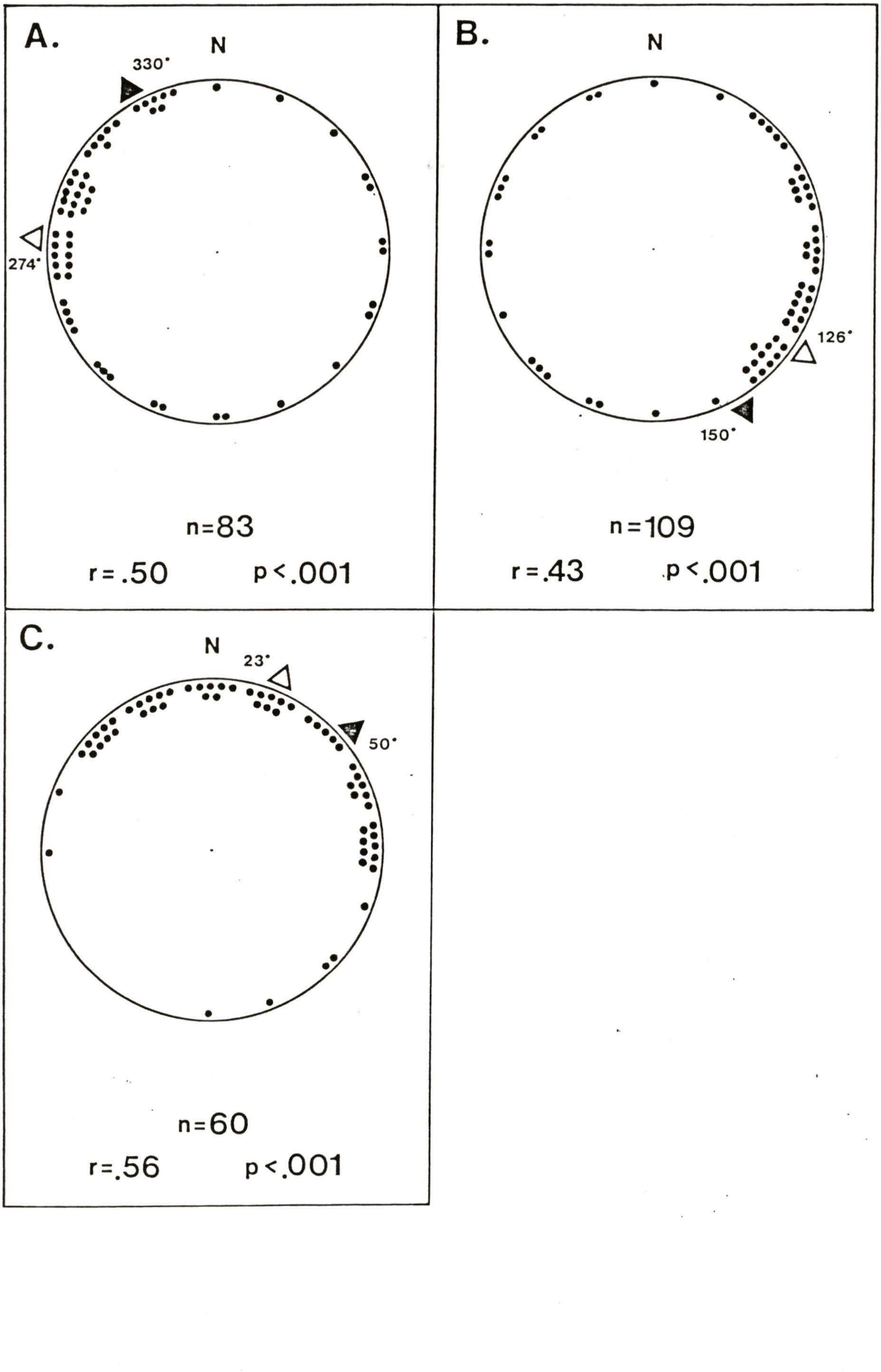
1) Daytime tests.

Daytime orientation tests with the Nanaimo populations were conducted under relatively clear (0-50% overcast) skies between 1155h - 1605h from June 12 to July 6, 1984.

The 3 populations showed highly significant orientation ($p < .001$), and all mean bearings were in the general seaward Y-axis directions (table 2, fig. 6a-c). The Rocky Point stock (Y-axis = 330°N) was strongly oriented offshore along 274°N, but this bearing was 56° counterclockwise and significantly different from the seaward Y-axis direction (C.I. test $p < .01$) (fig. 6a). The P.B.S beach stock was also concentrated in the seaward direction with a mean bearing of 126°N, but this was significantly different from the seaward Y-axis direction (C.I. test $p < .01$) (fig. 6b). The Piper's beach stock had a mean bearing of 23°N, significantly different from the seaward direction of 50°N (C.I. test $p < .01$) (fig. 6c). These results indicate that *H. nudus* from the Nanaimo area perform a seaward orientation under low cloud cover (0-50% overcast) in experimental arenas, which in some cases deviates from the seaward Y-axis direction.

The directions of the home beaches from the testing location were 256°N for the P.B.S. beach stock, 30°N for the Piper's beach stock, and 317°N for the Rocky Point crabs. Since the home directions for the Rocky Point and Piper's beach were close to the seaward Y-axis directions, the possibility of homing can not be excluded for these 2 stocks. However, since a homing direction was not evident for the P.B.S. beach crabs, I conclude that homing did not occur.

Figure 6. Daytime orientation of Nanaimo crab populations; (a): Test #101, Rocky Point (Y-axis = 330°N) stock, (b): Test #103, P.B.S. beach (Y-axis = 150°N) crabs, and (c): Test #110, Piper's beach (Y-axis = 50°N) stock, tested under a relatively clear sky. Each dot represents an individual's directional preference, solid triangles indicate expected directions (seaward Y-axis), open triangles signify mean bearings, n = number of individuals tested. Significance levels are based on the Rayleigh test.


A.
N
330°
274°
n=83
r=.50
p<.001
B.
N
126°
150°
n=109
r=.43
p<.001
C.
N
23°
50°
n=60
r=.56
p<.001

i) Effect of sample size on Y-axis orientation:

The 3 tests performed above, #101, #103, and #110 were further analyzed to determine what sample size was needed to obtain significant orientation.

After each 10 crabs tested, the mean bearing and r-values were calculated for the group, separately and cumulatively. Analysis of the cumulative sample determined at which sample size a daytime test would show statistically significant results. Comparison of individual groups and cumulative samples provided insight into the fluctuations of the mean bearing, r-value, and probability during testing (table 3).

In test #101 with the Rocky Point stock a total of 80 crabs were tested. Each group of 10 crabs had mean bearings ranging from 245°N-311°N (table 3(a), fig. 7a). The r-value fluctuated among the groups of 10 crabs (range of r = .23-.79), and 5 of the 8 groups were significantly different from uniformity.

The cumulative sample became statistically significant at the 20 crab sample size, and remained highly significant as sample size increased. The r-value of the cumulative sample varied from .23 to .53, and significantly increased with increasing sample size (ANOVA $p < .05$) (table 3(b), fig. 7a). The reason for this increase is not known. The mean bearing of the cumulative sample ranged from 268°N-311°N and did not change appreciably after about the 20 crab sample size. The mean bearings of the cumulative sample were not significantly different from each other (Watson-Williams analysis $p > .25$). Thus in this test, a sample of 20 crabs gave a statistically significant mean bearing.

The results of tests #103 with 100 crabs and #110 with 60 crabs were very similar to those of test #101. The separate group mean bearings in test #103 were all in the S.E. quadrant with mean directional choices ranging from 81°N-167°N. Only 4 out of 10 of the choice distributions

Table 3: Effect of sample size on Y-axis orientation in 3 Nanaimo populations and consistency of the mean bearing, r-value, and probability for successive tests with groups of 10 crabs each. n = sample size, mean bearings are in °N, and p = probability.

test #: 101 Rocky Point stock (Y-axis = 330°N)

a) separate group calculations				b) cumulative calculations			
n	mean bearing	r-value	p	n	mean bearing	r-value	p
0 - 10	311	.23	> .50	10	311	.23	> .50
11 - 20	279	.79	< .001	20	286	.49	< .01
21 - 30	245	.47	> .10	30	273	.46	< .002
31 - 40	266	.32	> .20	40	271	.42	< .001
41 - 50	266	.60	< .05	50	270	.46	< .001
51 - 60	262	.68	< .01	60	268	.49	< .001
61 - 70	294	.69	< .01	70	273	.51	< .001
71 - 80	274	.62	< .02	80	273	.53	< .001

test #: 103 P.B.S. beach stock (Y-axis = 150°N)

c) separate group calculations

n	mean bearing	r-value	p
0 - 10	167	.31	> .20
11 - 20	114	.46	> .10
21 - 30	111	.44	> .10
31 - 40	93	.13	> .50
41 - 50	81	.59	< .05
51 - 60	86	.93	< .001
61 - 70	162	.53	> .05
71 - 80	151	.26	> .50
81 - 90	133	.70	< .005
91 - 100	153	.70	< .005

d) cumulative calculations

n	mean bearing	r-value	p
10	167	.31	> .20
20	135	.35	> .05
30	126	.37	< .02
40	122	.30	< .05
50	110	.33	< .005
60	101	.42	< .001
70	111	.41	< .001
80	114	.38	< .001
90	117	.41	< .001
100	123	.43	< .001

test #: 110 Piper's beach stock (Y-axis = 50°N)

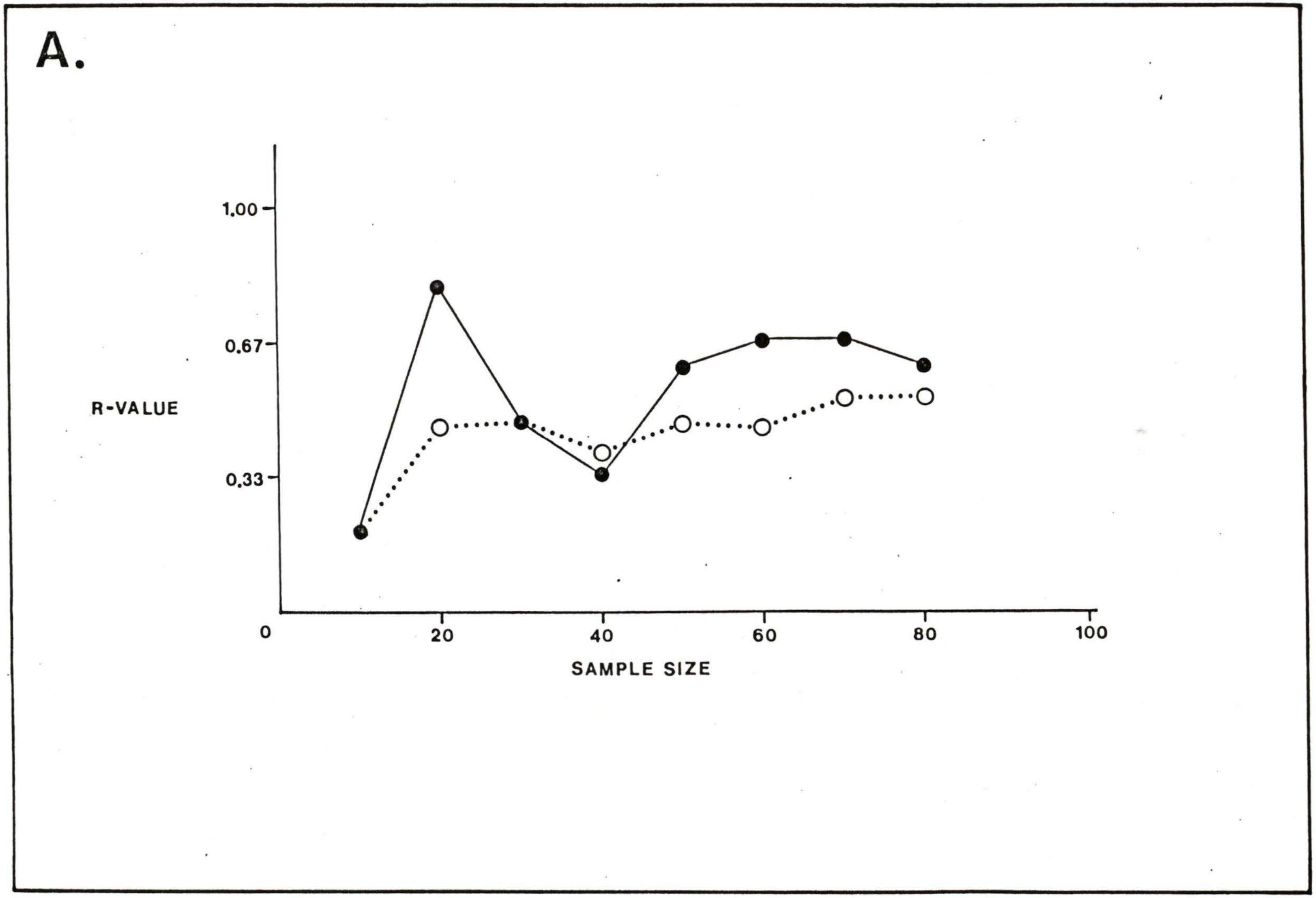
e) separate group calculations

n	mean bearing	r-value	p
0 - 10	33	.60	< .05
11 - 20	19	.58	< .05
21 - 30	47	.47	> .10
31 - 40	12	.74	< .002
41 - 50	31	.47	> .10
51 - 60	4	.60	< .05

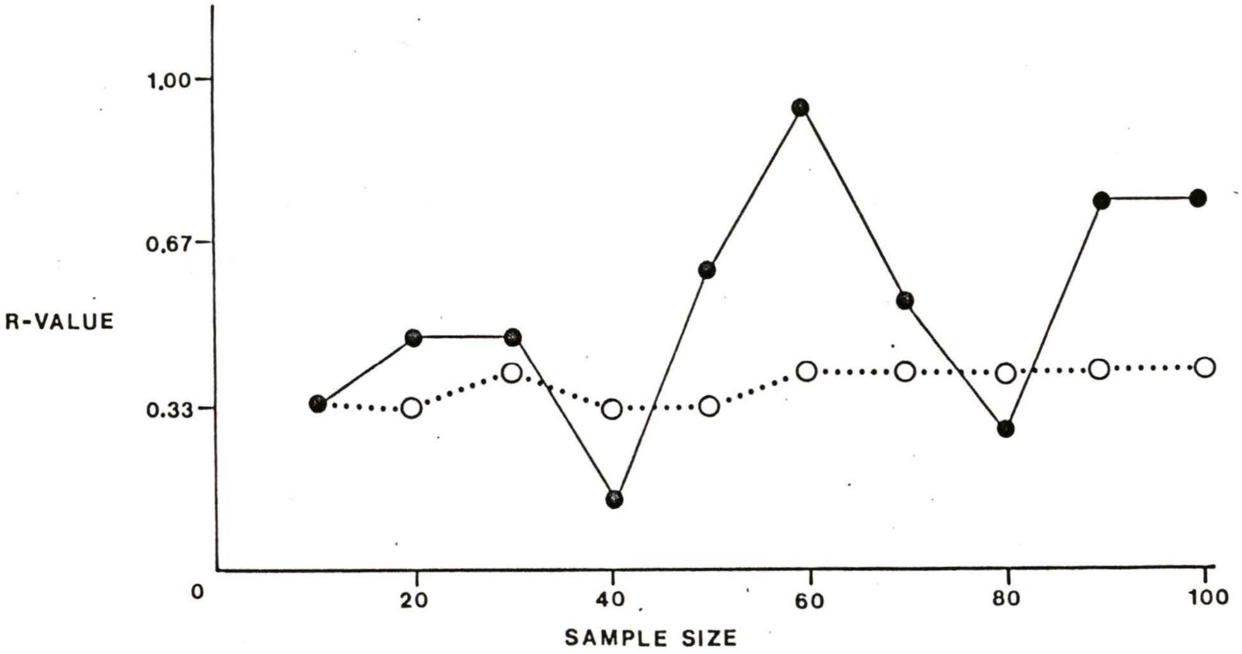
f) cumulative calculations

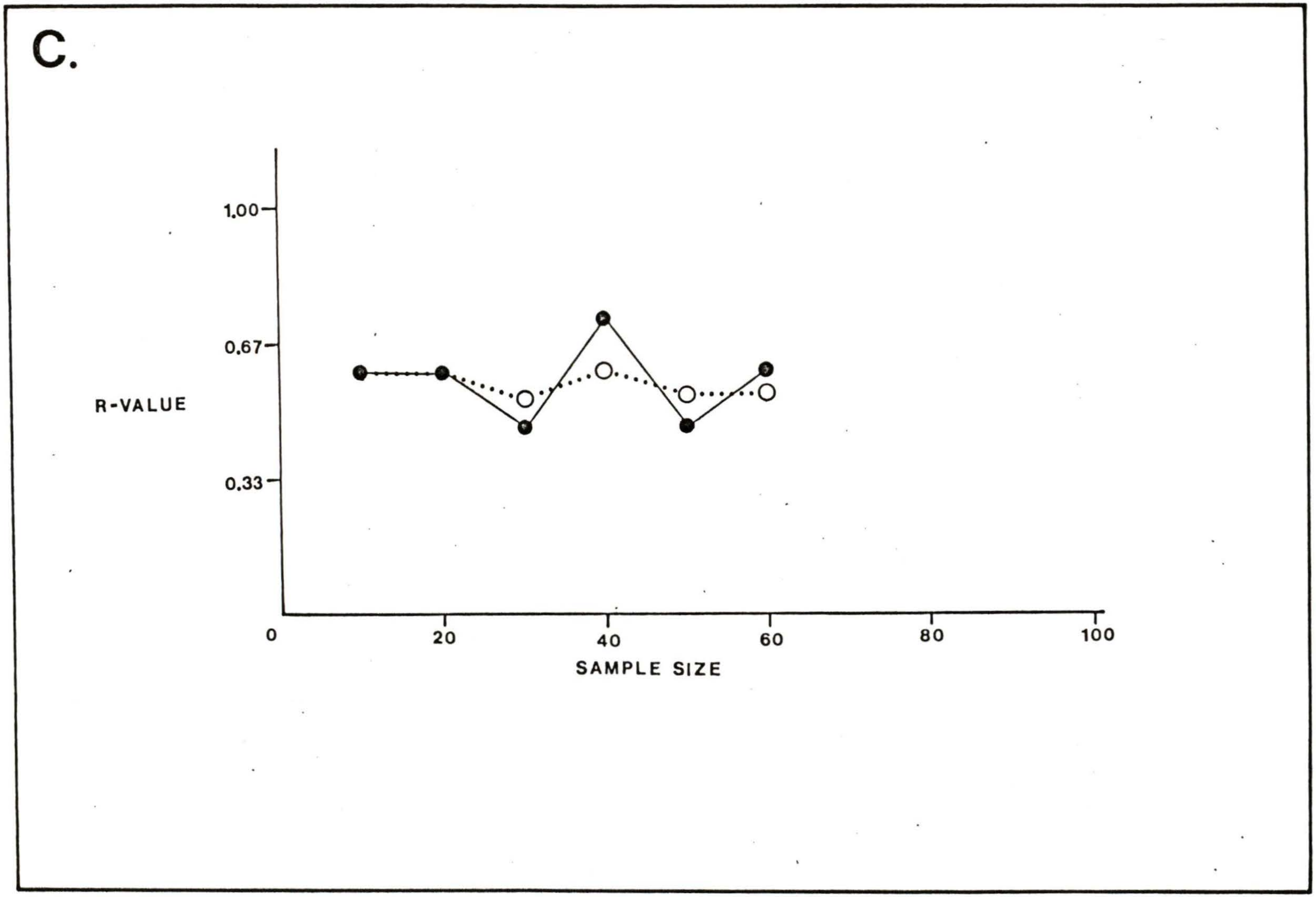
n	mean bearing	r-value	p
10	33	.60	< .05
20	26	.59	< .001
30	32	.54	< .001
40	26	.58	< .001
50	27	.56	< .001
60	23	.56	< .001

Figure 7. Effect of sample size on Y-axis orientation in 3 Nanaimo populations, and consistency of the mean bearing, r-value and probability for successive tests with groups of 10 crabs each. Separate group mean bearings are denoted by solid cicles and lines, cumulative mean bearings are indicated by open circles and dashed lines, for (a): Test #101, Rocky Point (Y-axis = 330°N) crabs, (b): Test #103, P.B.S. beach (Y-axis = 150°N) crabs, and (c): Test #110, Piper's beach (Y-axis = 50°N) crabs.


A.
1.00
0.67
R-VALUE
0.33
0
20
40
60
80
100
SAMPLE SIZE

B.




C.
R-VALUE
1.00
0.67
0.33
0
20
40
60
80
100
SAMPLE SIZE

were significantly different from uniformity (table 3(c), fig. 7b). The cumulative sample became statistically significant at the 30 crab sample size (table 3(d), fig. 7b). Fluctuations in the cumulative sample were similar to those of the previous test. The r-value (range = .30-.43) again significantly increased with increasing sample size (ANOVA $p < .01$). The cumulative sample mean bearings (range = 101°N-167°N) in this test were not significantly different (Watson-Williams analysis $p > .25$) and the mean bearing stabilized after 30 crabs were tested. Thus a sample size of 30 crabs would have been sufficient to detect statistically significant orientation.

Individual groups of 10 crabs in test #110 varied in mean bearing from 4°N-47°N (table 3(e), fig. 7c). Four of the 6 groups showed significant orientation. The cumulative sample was statistically significant at the 10 crab sample size and remained highly significant for the remainder of the test. The mean bearing (23°N-33°N) fluctuated minimally (10°) in this test, and did not significantly change with increasing sample size (Watson-Williams analysis $p > .25$) (table 3(f), fig. 7c). The r-value (range = .54-.60) also did not significantly change with increasing sample size (ANOVA $p > .25$). These results suggest that the sample of even 10 crabs would have been sufficient in this test.

The r-value is not dependent on sample size. Thus an increase in r-value in tests #101 and #103 indicates an improvement in directionality with increasing sample size. The reason for this is not clear. The p-value in all tests decreased with increasing sample size, since it is inversely related to sample size and also to the r-value.

A sample size of 30 crabs would have been sufficient to detect statistically significant orientation in all tests. However, since the highest value of statistical significance for the mean bearing which can be read from statistical tables was reached at about the 60 crab sample size in the worst case (test #103), I decided to set the sample size at 50-60 crabs per test.

ii) Effect of sex and size on Y-axis orientation:

Tests #101, #103, and #110 were also used to determine possible size and sex differences in Y-axis orientation. The crabs were collected as randomly as possible without an obvious sex or size bias and were sexed and measured after testing to the nearest 0.01 cm across the widest part of the carapace. The sexes and size groups were then independently analyzed for mean bearings using the Rayleigh test. The results of the calculations were compared to each other using the Watson-Williams analysis to detect significant differences in orientation direction between the groups. The directional results of the males and females are presented in table 4.

The statistical significance for directionality was high ($p < .001$) in every group. The mean bearings and r-values were very similar for the different sexes within each experiment, even though the sample size for males and females was dissimilar in tests #101 and #103 (table 4). No sex-based differences in directional preferences were found using the Watson-Williams analysis; test #101 ($p > .25$), test #103 ($p > .25$), and test #110 ($p > .05$), and the r-values of the males and females (range = .45-.59) were also not significantly different (r-value test $p > .25$). These results indicate that the directional choices of both males and females can be pooled.

Crabs from each test were divided into 4 size categories, with similar numbers of animals (irrespective of sex) in each category. The size classes were not divided into consistent size ranges due to a different relative abundance of various sized individuals at the 3 collection sites. The results of the size split are presented in table 5.

The 3 smaller size classes of the Rocky Point stock (test #101) all had highly significant orientation in similar directions, ranging from 273°N-280°N (table 5). Orientation in the largest group was not significantly different from uniformity ($p > .05$). The reason for the lack of orientation in this group is not known.

Table 4: Effect of crab sex on Y-axis orientation. n = sample size, Y-axes and mean bearings are in °N, and p = probability.

test #	stock	group split (sex)	n	Y-axis	mean bearing	r-value	p
101	Rocky Point	males	61	330	279	.47	< .001
		females	22		278	.59	< .001
103	P.B.S. beach	males	69	150	126	.45	< .001
		females	39		124	.42	< .001
110	Piper's Beach	males	26	50	26	.48	< .001
		females	34		22	.59	< .001

All 4 size groups of the P.B.S. beach stock (test #103) had significant mean bearings in directions which varied from 106°N-157°N (mean = 126N) and had similar r-values (range .42-.50) (table 5).

The 3 smallest size groups of the Piper's beach stock (test #110) showed similar mean bearings ranging from 20°N-51°N (table 5). The mean bearing of the largest group was 344°N. Note that it was also the largest group in test #101 that showed an orientation quite different from the 3 smaller sizes. However, the Watson-Williams analysis on each population showed that the differences in the orientation direction between various sized individuals were not significant; test #101 (p> .25), test #103 (p> .10), and test #110 (p> .05). Also, there was no significant difference in the concentration of choices (r-values) between the different size groups (p> .25). I thus conclude that crab size does not affect the mean bearing or the strength of the orientation, and that the results of crabs of different sizes can be pooled.

2) Nighttime tests.

Tests at night were performed with the 3 Nanaimo populations (Rocky Point, P.B.S. beach and Piper's beach stock) under slightly overcast skies and no moon, between 0025h - 0335h from June 25 to July 8, 1984. The results of these tests are presented in table 6.

Test #112B was performed under a 40% overcast sky after the moon had set and produced a highly significant mean bearing of 21°N (p< .001), which was 51° clockwise, and significantly different from the seaward Y-axis direction of 330°N (C.I. test p< .01) (table 6, fig. 8a). Although the crabs' orientation would have led them in general towards water, it was not close to the seaward Y-axis direction.

Test #107 with the P.B.S. stock on a moonless night produced a highly significant mean bearing of 121°N (p< .02), 29° clockwise, and not

Table 5: Effect of crab size on Y-axis orientation. n = sample size, Y-axes and mean bearings are in °N, and p = probability.

test #	stock	group split (size) (cm)	n	Y-axis	mean bearing	r-value	p
101	Rocky Point	1.30 <x< 1.79	29	330	278	.52	< .001
		1.80 <x< 1.90	18		273	.53	< .005
		1.90 <x< 2.09	17		280	.62	< .001
		2.10 <x< 3.00	19		74	.30	> .05
103	P.B.S. beach	1.00 <x< 1.39	30	150	127	.43	< .002
		1.40 <x< 1.59	30		106	.50	< .001
		1.60 <x< 1.79	24		157	.43	< .02
		1.80 <x< 2.39	24		131	.42	< .02
110	Piper's beach	1.00 <x< 1.29	14	50	20	.60	< .005
		1.30 <x< 1.39	14		37	.48	< .05
		1.40 <x< 1.59	17		51	.61	< .002
		1.59 <x< 2.30	15		344	.45	< .05

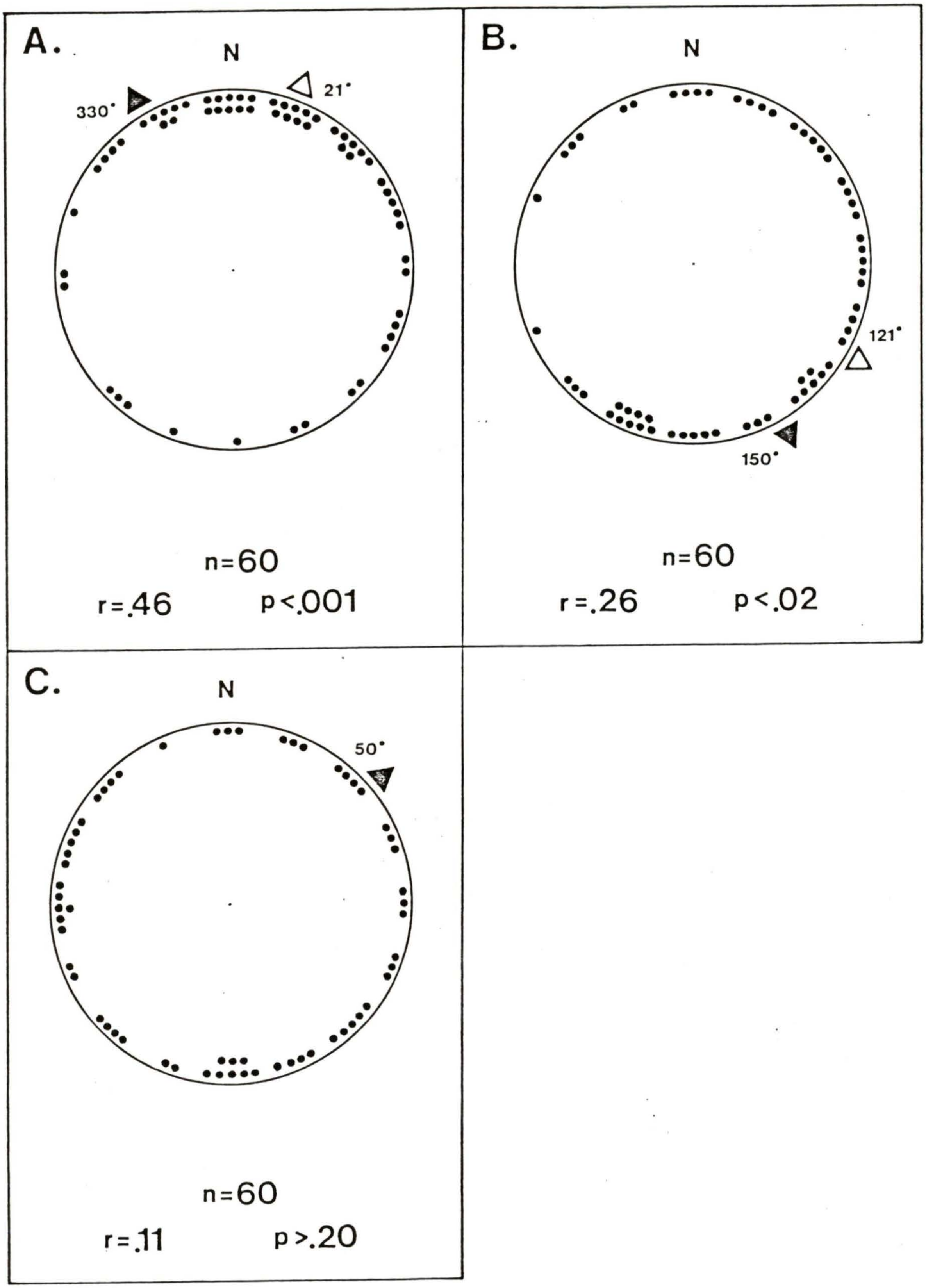
Table 6: Results of nighttime orientation tests with 3 Nanaimo crab populations in the absence of a moon. n = sample size, Y-axes and mean bearings are in °N, and p = probability.

test #	stock	% overcast	n	Y-axis	mean bearing	r-value	p
112B	Rocky Point	40%	60	330	21	.46	< .001
107	P.B.S. beach	0%	60	150	121	.26	< .02
109B	Piper's beach	10%	60	50	195	.11	> .20

Table 7: Orientation of crabs from 29th Street beach, West Vancouver. n = sample size, X-axis and mean bearings are in °N, and r-value and probability (p) are based on the bimodal Rayleigh test.

test #	% overcast	X-axis	bimodal mean bearing	n	r-value	p
91	0%	125 & 305	145 & 325	25	.22	> .20
94	50%	"	128 & 308	54	.21	> .10
97	100%	"	116 & 296	35	.25	> .10
pooled data		125 & 305	127 & 307	114	.21	< .01

Figure 8. Results of nighttime orientation tests with 3 Nanaimo crab populations in the absence of a moon, under a relatively clear sky; (a): Test #112B, Rocky Point (Y-axis = 330°N) crabs, (b) Test #107, P.B.S. beach (Y-axis = 150°N) stock, and (c) Test #109B, Piper's beach (Y-axis = 50°N) crabs. Legend as in fig. 6.


A.
N
330°
21°
n=60
r=.46
p<.001
B.
N
121°
150°
n=60
r=.26
p<.02
C.
N
50°
n=60
r=.11
p>.20

different from the seaward Y-axis of 150°N (C.I. test p> .05) (fig. 8b), indicating that this stock is capable of seaward Y-axis orientation at night.

Test #109B was conducted with the Piper's beach stock under a 10% overcast night sky after the moon had set. The animals in this test showed orientation not different from uniformity (p> .20) (fig. 8c).

Comparison of the daytime (#110) and nighttime (#109B) tests of the Piper's beach crabs showed that they had a seaward and landward Y-axis orientation, respectively. Also, the r-values of the 2 tests were significantly different (r-value test p< .005), indicating that this stock had significantly less directed orientation at night than during the day.

Analysis of the r-values of day and night tests with the Rocky Point stock (tests #101 and #112B, respectively) and the P.B.S. beach stock (tests #103 and #107, respectively) showed no significant differences (r-value test p> .25, and p> .05, respectively), suggesting that the Rocky Point and P.B.S. beach crabs are capable to orient equally well at night as during the day.

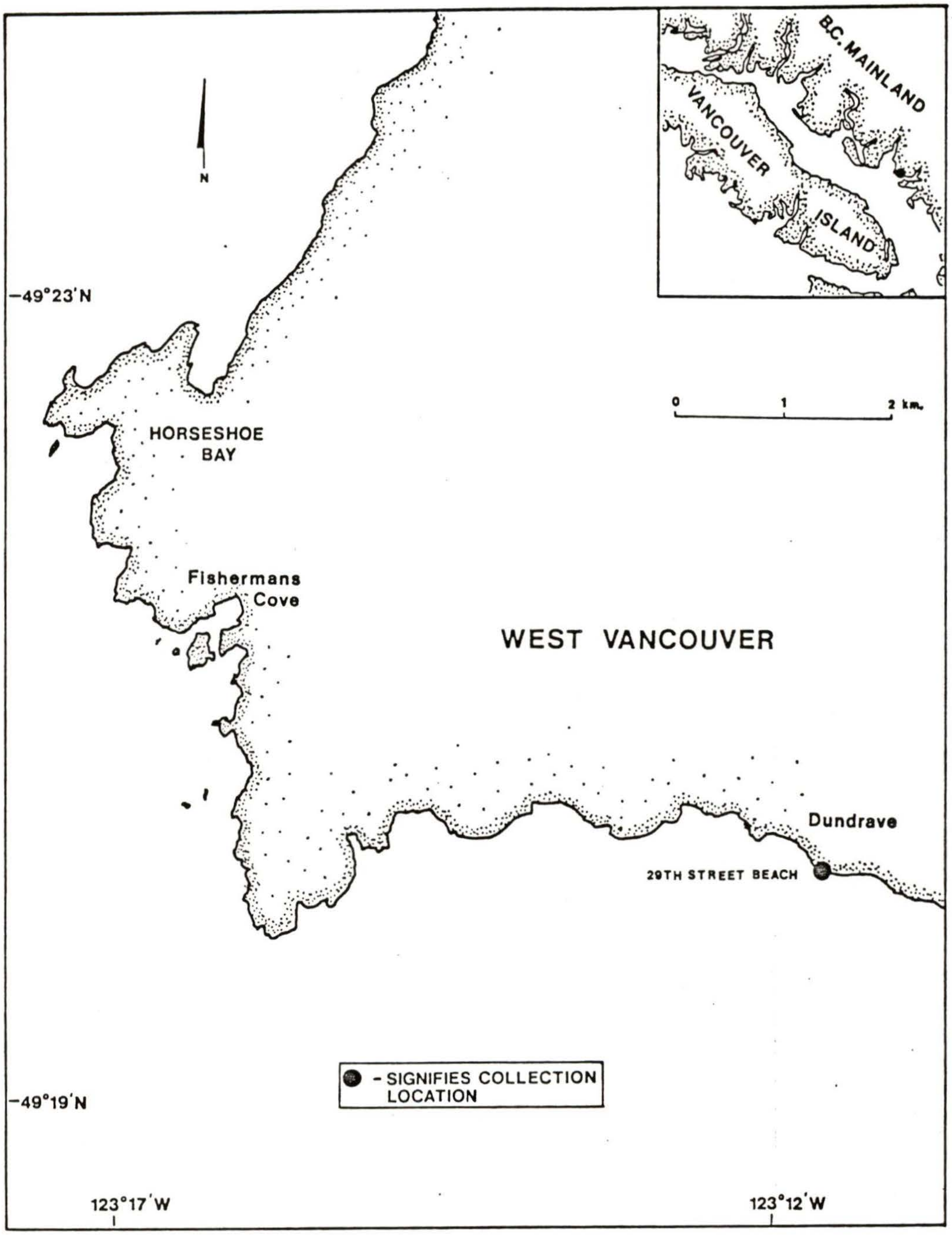
C. VANCOUVER TESTS

EXPERIMENTAL PROCEDURE

Crabs were collected from West Vancouver's 29th street beach (Y-axis = 215°N, X-axis = 125°N and 305°N) (fig. 9) and were transported to the testing area by car in 20 l collection buckets with lids. They were held indoors in 250 gallon barren, oval, light blue fiberglass tanks with running sea water, for less than 24 h prior to testing, at the Deptartment of Fisheries and Oceans' West Vancouver Laboratory.

Four experiments were performed between 1330h - 1630h, during Feb. 16-24, 1984, on the West Vancouver Laboratory boat dock. The test area

Figure 9. Collection area in West Vancouver, B.C. Source: Canadian Hydrographic Service, D.F.O., Ottawa, 1978.


N
B.C. MAINLAND
VANCOUVER
ISLAND
-49°23'N
0
1
2 km.
HORSESHOE
BAY
Fishermans
Cove
WEST VANCOUVER
Dundrave
29TH STREET BEACH
● - SIGNIFIES COLLECTION
LOCATION
-49°19'N
123°17'W
123°12'W

was located approximately 5 m from the shoreline. Orientation arena #2 and the support table were used. The animals were tested singly and each crab was given a period of 1 min in the ring and 1 min after release to make a trap choice. It was not possible to test 50-60 crabs in every experiment due to changing weather conditions during testing.

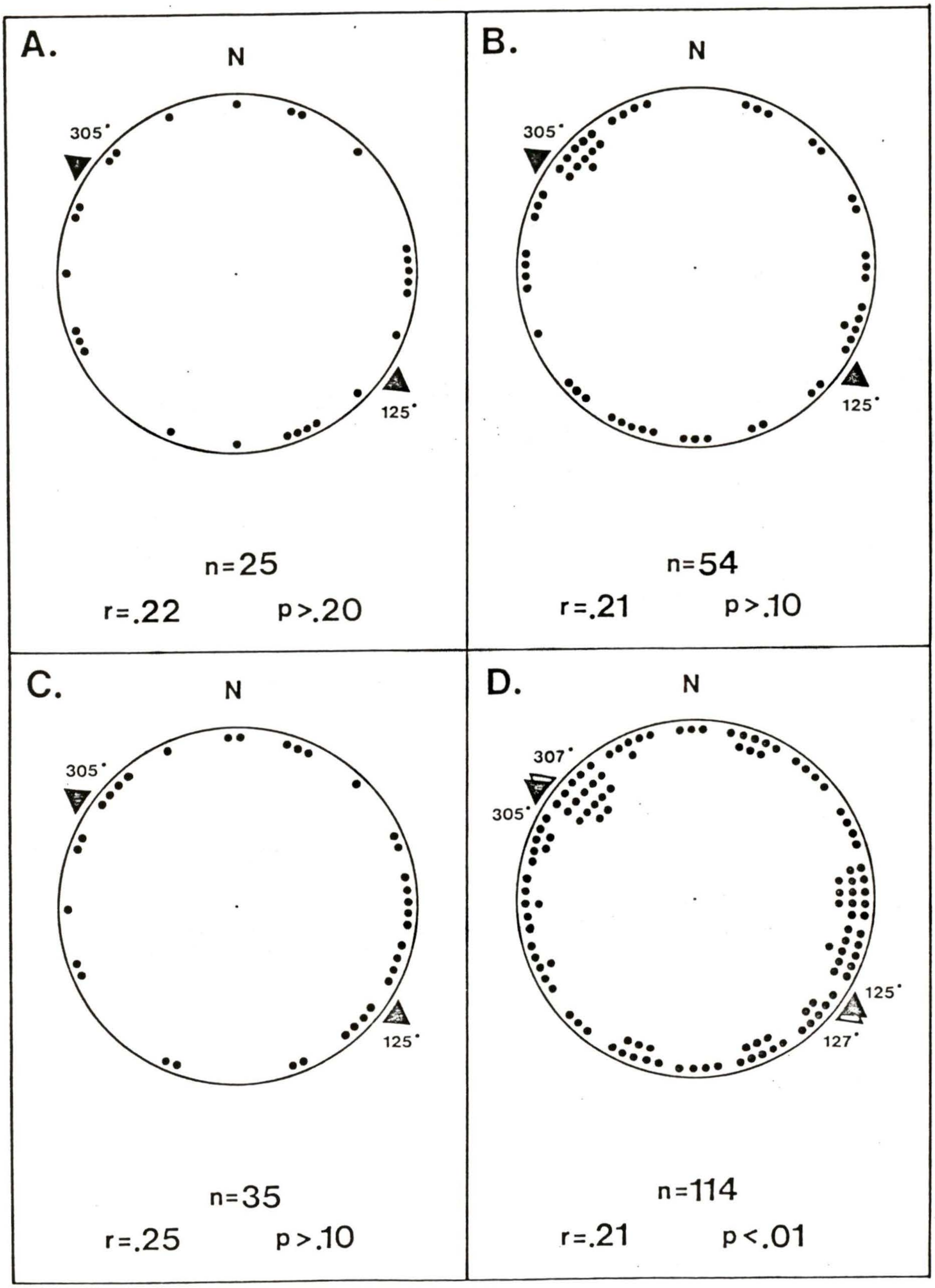
RESULTS

Results of the tests with the Vancouver crabs are presented in fig. 10 and table 7. The 3 experiments produced bimodal mean bearings of 145°N and 325°N, 128°N and 308°N, and 116°N and 296°N, which although not significantly different from uniformity ($p > .10$ to $p > .20$) were very similar to the X-axis directions of 125°N and 305°N for the 29th Street beach (table 7, fig. 10a-c).

The mean bearings of the 3 tests are not significantly different from each other (Watson-Williams analysis $p > .10$). Pooling the tests resulted in a significant bimodal mean bearing of 127°N & 307°N ($p < .01$) (fig. 10d), close to the beach X-axis of 125°N and 305°N. The possibility of homing was excluded since the compass direction of the home beach from the West Vancouver Laboratory testing area is 104°N. Thus *H. nudus* from the West Vancouver area orient parallel to their home beach in both directions under experimental conditions.

Four populations of *H. nudus* from the Vancouver area have been previously tested by van Tets (1956) with respect to their beach directed orientation. He also found that the crabs orient to the X-axes of their home beaches rather than to the Y-axes. His studies are the only known record of previous orientation experiments done with this species, and since then *H. nudus* has been regarded as performing only X-axis orientation in the literature (ie. Pardi and Papi, 1961; Herrnkind, 1972; Nishimoto and Herrnkind, 1982; misinterpretted in Herrnkind, 1983).

Figure 10. Orientation of crabs from 29th Street beach, West Vancouver, (X-axis = 125°N & 305°N) tested under variable overcast; (a-c): replicate tests #91, #94, #97 respectively, (d) pooled results of a-c. Bimodal expected directions represent X-axis. Other legend as in fig. 6.


A.
N
305°
125°
n=25
r=.22 p>.20
B.
N
305°
125°
n=54
r=.21 p>.10
C.
N
305°
125°
n=35
r=.25 p>.10
D.
N
307°
305°
125°
127°
n=114
r=.21 p<.01

I reanalyzed van Tets' (1956) data since he did not use statistical analyses which are now available and erroneously pooled all of the position records from all individuals from the same beach, which were not statistically independent from each other. From first-order vectors calculated for each crab with the Rayleigh test, the second-order vector was then determined. The results of these calculations show that the majority of individuals were orienting along one or both of the X-axis directions of the respective beaches. It must however be emphasized that my conclusions may not be totally valid, since statistical independence of successive position records could not be established in van Tets' data. Hamilton (1966) and Simpson (1979) both pointed out the importance of independence in successive orientation records of one individual, before subjecting the data to statistical analyses. Thus my investigation of the orientation of the Vancouver populations confirms van Tets' (1956) findings of almost 30 years ago.

SUMMARY

The populations of H. nudus from the Bamfield and Nanaimo areas all orient seaward when tested in orientation arenas under relatively clear day skies (0-50% overcast). However, the mean bearings appear to be prone to significant deviation from the seaward Y-axis directions. Two of the 3 Nanaimo populations (Rocky Point and P.B.S. beach) showed Y-axis orientation at night under relatively clear skies (0-40% overcast), in the absence of a moon.

The West Vancouver population performed bimodal X-axis orientation when tested under 0-100% overcast day skies in an orientation arena. These results are consistent with van Tets' (1956) observations.

The crabs in all populations did not home.

The seaward Y-axis orientation ability in the Nanaimo crabs is independent of the sex and size of the individuals.

The sample size affects the mean bearing and orientation strength, which fluctuate with increasing sample size.

The crab sample size chosen for further testing was set at 50-60 animals.

PART 2. FACTORS AFFECTING Y-AXIS ORIENTATION

V. SOME FACTORS AFFECTING Y-AXIS ORIENTATION

INTRODUCTION

In the previous chapter I have shown that _H. nudus_ from the Bamfield and Nanaimo areas perform Y-axis orientation when tested in arenas, while _H. nudus_ from the Vancouver area perform X-axis orientation.

In this chapter information will be given on the effects of the time of day, temperature, tidal cycles, level of activity, the moon, position of the observer, and sky blockage, on the strength, and mean bearing of Y-axis orientation. The same experimental procedure was used as described in the previous chapters. Specific information related to each testing procedure will be presented in the appropriate sections.

RESULTS

a) Factors influencing the seaward Y-axis orientation and strength (r-value).

1) Diel effects.

Crabs from the P.B.S. beach (Y-axis = 150°N) were tested in 5 consecutive experiments spaced out over a 24 h period on July 16 and 17, 1984, under clear (0% overcast) day and night skies to determine if changes occur in the orientation at different times of the diel cycle. Orientation arena #2 and the support table were used. Crabs were tested singly and given 30 s in the ring and 30 s to make a trap choice after release.

Tests were performed during sunset (2024h) and sunrise (0430h), since these times were considered to be important due to the changing sky at those times, and mid-afternoon (1624h, medially between mid-day and sunset), mid-night (0019h, medially between sunset and sunrise), and mid-morning (0837h, medially between sunrise and mid-day). Times for sunset and sunrise were obtained from tables in the Nautical Almanac (1983), and all other times were extrapolated from these. The period of testing was approximately centered over the exact times of sunrise, sunset, and the other chosen points in the diel cycle. Testing during sunrise was completed before the sun was visible on the horizon and testing during the sunset period started after the sun had set on the horizon.

The crabs in all of the tests had highly significant mean bearings (table 8, fig. 11a-e). The mean bearings ranged from 93°N (mid-morning) to 187°N (mid-afternoon) and thus deviated up to 57° eastward from the seaward Y-axis direction of 150°N. The mean bearings of the sunset (#115) (fig. 11b), midnight (#116) (fig. 11c), and mid-morning test (#118) (fig. 11e) differed significantly from the seaward Y-axis direction (C.I. test $p< .01$), while the sunrise (#117) (fig. 11d) and mid-afternoon tests (#114) (fig. 11a) had mean bearings not significantly different from the seaward Y-axis direction (C.I. test $p> .05$). The pooled mean bearing of 140°N of all tests was in the seaward Y-axis direction of 150°N (C.I. test $p> .05$), suggesting that the mean bearing fluctuates about the seaward Y-axis direction.

To determine if significant changes in the orientation strength occured during the different testing periods, bearing deviation tests were used to compare the r-values of successive experiments. Comparison of the r-values of the 5 tests (r-value test) indicated no significant difference between r-values of successive tests (r-value tests $p> .05$ to $p> .25$) (table 9) or between any 2 of the 5 tests (r-value test $p> .05$). This suggests that the strength of orientation in this series does not change with time of day and that the directional choice is independent of the strength of the orientation. This is important since it indicates that crabs in tests in which the mean bearing is close to the Y-axis direction are not necessarily

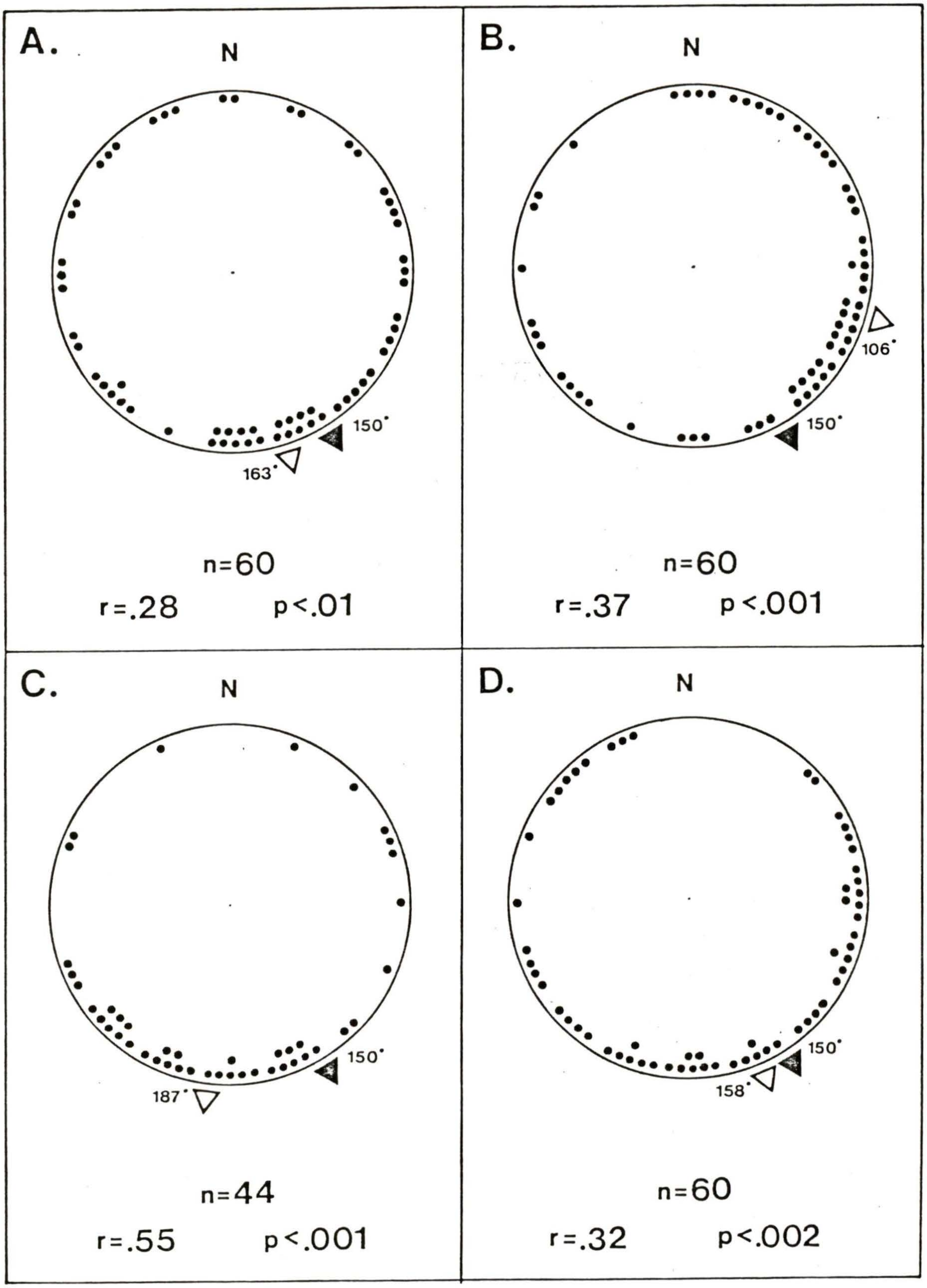
Table 8: Directional tendencies of _H. nudus_ from the P.B.S. beach (Y-axis = 150°N) tested at different times during a 24 h period. n = sample size, Y-axis and mean bearings are in °N, and p = probability.

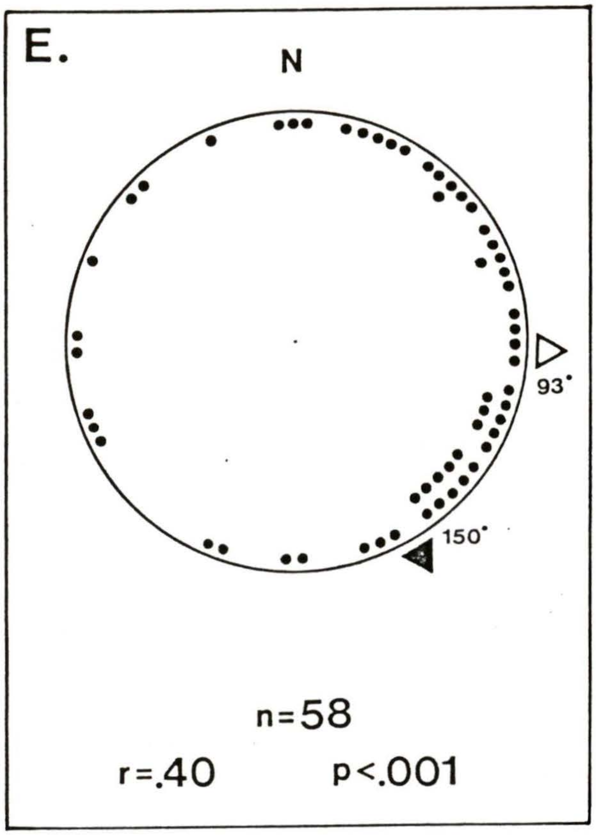
test #	test condition	start of test (h)	n	Y-axis	mean bearing	r-value	p	p of C.I. test
114	mid-afternoon	1624h	60	150	163	.28	< .01	> .05
115	sunset	2024h	60	150	106	.37	< .001	< .01
116	mid-night	0019h	44	150	187	.55	< .001	< .01
117	sunrise	0430h	60	150	158	.32	< .002	> .05
118	mid-morning	0837h	58	150	93	.40	< .001	< .01

Table 9: Results of Watson-Williams analyses and r-value tests to determine significant differences in orientation between successive tests (significance represents difference). p = probability.

successive test pairs	p of mean bearings	p of r-values
#114 mid-afternoon and #115 sunset	p< .01	p> .25
#115 sunset and #116 mid-night	p< .001	p> .10
#116 mid-night and #117 sunrise	p> .05	p> .05
#117 sunrise and #118 mid-morning	p< .001	p> .25
#118 mid-morning and #114 mid-aft.	p< .001	p> .25

Figure 11. Directional tendencies of H. nudus from the P.B.S. beach (Y-axis = 150°N) tested at different times during a 24 h period; (a): Test #114, mid-afternoon, (b): Test #115, sunset, (c): Test #116, mid-night, (d): Test #117, sunrise, (e) Test #118, mid-morning. Legend as in fig. 6.


A.
N
150°
163°
n=60
r=.28 p<.01
B.
N
106°
150°
n=60
r=.37 p<.001
C.
N
150°
187°
n=44
r=.55 p<.001
D.
N
150°
158°
n=60
r=.32 p<.002


E.
N
93°
150°
n=58
r=.40
p<.001

more strongly oriented than crabs whose mean bearing deviated from the Y-axis direction.

To determine if significant changes in the mean bearigs occured during the different testing periods, Watson-Williams analyses were used to compare the mean bearings of successive experiments (table 9). The Watson-Williams analysis is sensitive to the orientation strength (r-value). However, the concentration factor was eliminated since the orientation strength was not significantly different among the tests, and the Watson-Williams analysis only compared mean bearings.

The analysis showed that most tests had significantly different mean bearings ($p < .001$), except for the mid-night and sunrise tests (#116 and #117), which did not ($p > .05$) (table 9). However, no correlation between the time of day and mean bearing is apparent (fig. 12).

From these results I conclude that directional preference of the crabs over a 24 h period is in the general direction of the seaward Y-axis and that no direct relationship is evident between the changes in mean bearing with time of day.

2) Effect of temperature on the directional preference.

Temperature variation during testing was recorded to determine if it was one of the factors affecting the directional preference (table 10).

The results showed that the mean bearings were not significantly correlated with temperature ($p > .20$) (table 10), indicating that the directional preference was not affected by temperature within the range encountered in these experiments.

Figure 12. Change in mean bearing over time for crabs tested at different times during a 24 h period. Letters refer to tests in fig. 11.

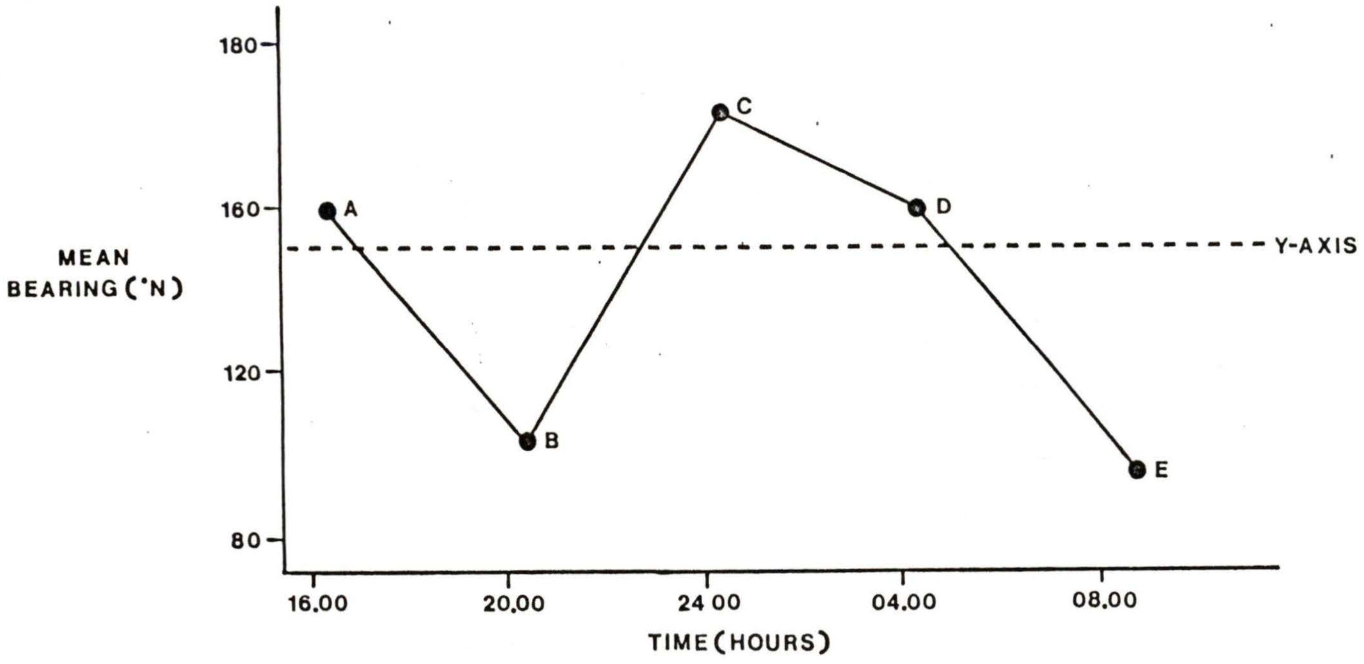

180
160
120
80
MEAN BEARING (°N)
A
B
C
D
E
Y-AXIS
16.00
20.00
24 00
04.00
08.00
TIME (HOURS)

Table 10: Temperature effects on the directional preference of *H. nudus* from the P.B.S. beach (Y-axis = 150°N) tested at different times during the diel cycle. Mean bearings are in °N.

test #	test condition	mean bearing	temperature (C)
114	mid-afternoon	163	34.0
115	sunset	106	27.5 - 23.0
116	mid-night	187	18.5 - 17.0
117	sunrise	158	16.0 - 14.5
118	mid-morning	93	19.5 - 29.0

Table 11: Tidal effects on the directional preference of crabs from the P.B.S. beach (Y-axis = 150°N) tested during a diel series of tests. Mean bearings are in °N.

test #	test condition	mean bearing	median test ht. (ft.)	tide type
114	mid-afternoon	163	8.0	flow
115	sunset	106	14.4	high
116	mid-night	187	12.1	ebb
117	sunrise	158	10.8	flow
118	mid-morning	93	9.7	ebb

3) Effect of tide on the directional preference.

The tidal cycle was another time-dependent variable analyzed to determine its effect on the orientation direction (table 11). The mean bearing was not significantly correlated with the tide height ($p > .25$) or period of the tidal cycle ($p > .20$) (table 11). I thus conclude that the mean bearing is not affected by tidal factors.

4) Effect of the moon on nighttime Y-axis orientation.

To determine the effect of the moon on the mean bearing and orientation strength, nighttime tests were performed with the moon present, with 3 Nanaimo stocks; Rocky Point, P.B.S. beach and Piper's beach stocks, under low overcast (0-40%) skies. The tests were carried out between 2255h - 0255h from June 13-July 17, 1984. The animals were tested singly in orientation arena #2 (including the support table) and were given 30 s in the ring and 30 s after release to make a trap choice. The results are presented in table 12.

Two tests with the Rocky Point stock (Y-axis = 330°N) were performed. Test #102 conducted under a full moon was random ($.06 > p > .05$) (table 12, fig. 13a). Test #112A performed under a 3/4 visible moon produced a highly significant mean bearing of 358°N, which was not significantly different from the seaward Y-axis direction of 330°N (C.I. test $p > .05$) (fig. 13b).

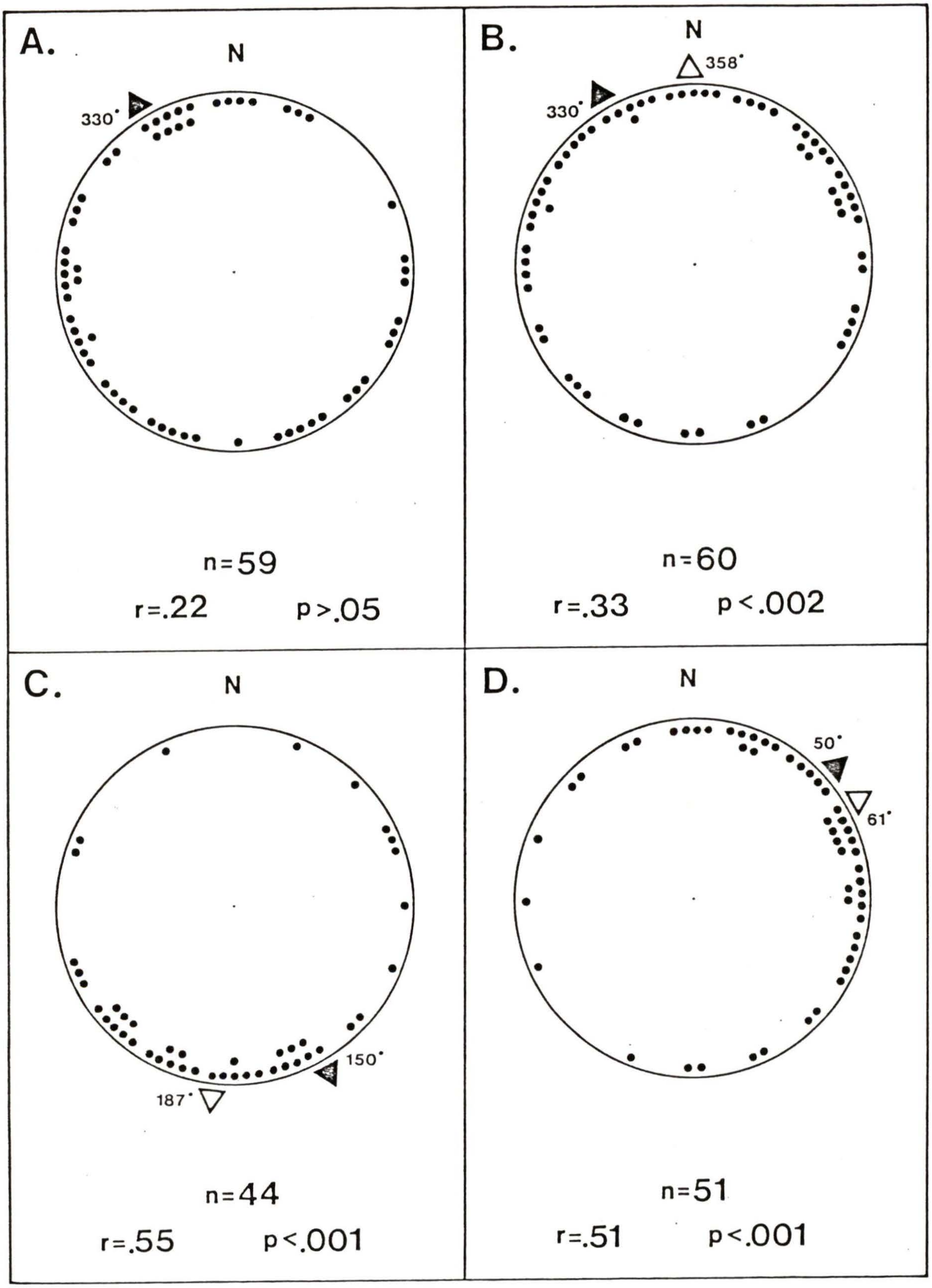
Test #116 with the P.B.S. stock was one from the series of 5 tests performed for the diel effects (Section 1, above) under a 3/4 visible moon. The highly significant mean bearing of 187°N ($p < .001$) was significantly different from the seaward Y-axis of 150°N (C.I. test $p < .01$) (fig. 13c). The reason for this is not known.

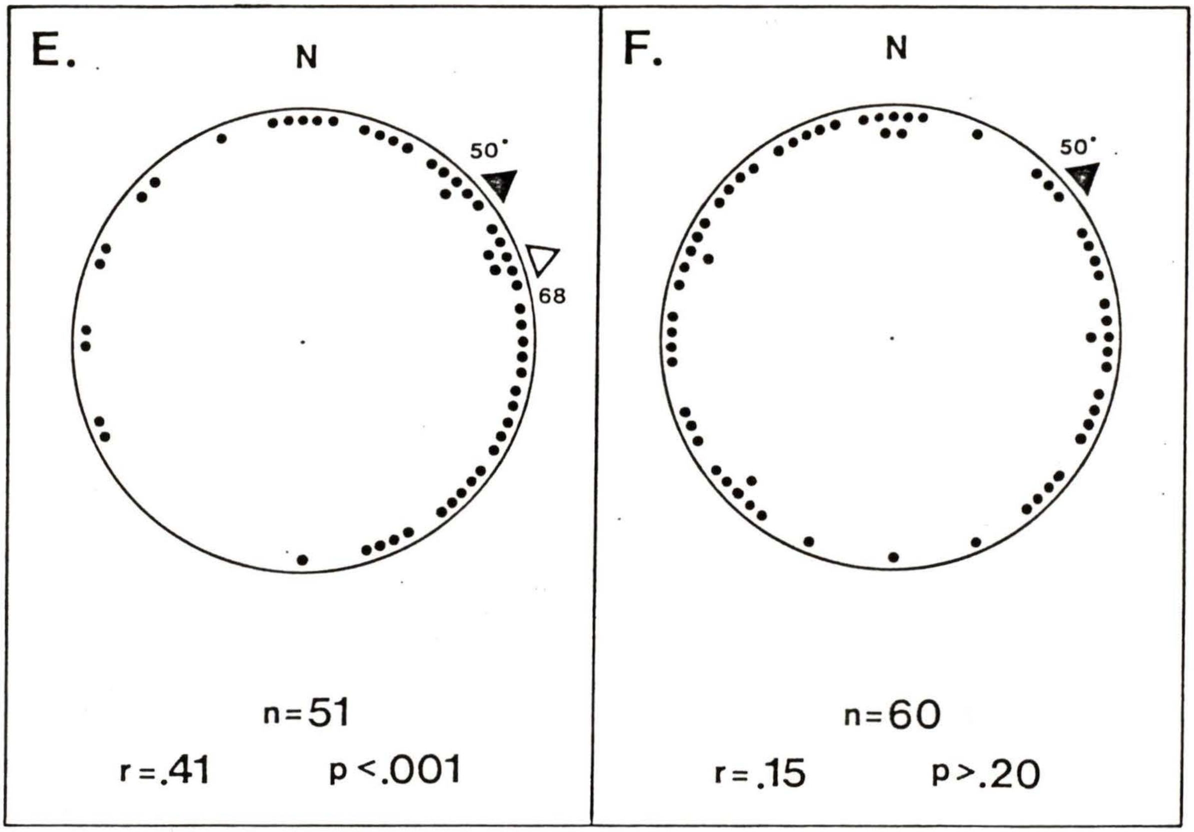
Table 12: Results of nighttime orientation tests with the moon visible for 3 Nanaimo crab populations. Moon's bearing, Y-axes, and mean bearings are in °N, n = sample size, and p = probability.

test #	stock	% overcast	moon phase	moon bearing
102	Rocky Point	0%	full	115-155
112A	Rocky Point	30%	first 3/4	148-172
116	P.B.S. beach	0%	last 3/4	80-109
113A	Piper's beach	0%	last 3/4	138-159
113B	Piper's beach	0%	last 3/4	159-188
109A	Piper's beach	40%	first 1/4	215-225

test #	n	Y-axis	mean bearing	r-value	p
102	59	330	267	.22	> .05
112A	60	330	358	.33	< .002
116	44	150	187	.55	< .001
113A	51	50	61	.51	< .001
113B	51	50	68	.41	< .001
109A	60	50	344	.15	> .20

Figure 13. Effect of the moon on nighttime Y-axis orientation. Results of nighttime orientation tests with the moon visible for 3 Nananimo crab populations; (a, b): Tests #102, #112A, Rocky Point (Y-axis = 330°N) crabs, (c): Test #116, P.B.S. beach (Y-axis = 150°N) animals, (d-f): Tests #113A, #113B, #109A, Piper's beach (Y-axis = 50°N) crabs. Legend as in fig. 6.


A.
N
330°
n=59
r=.22 p>.05
B.
N
358°
330°
n=60
r=.33 p<.002
C.
N
150°
187°
n=44
r=.55 p<.001
D.
N
50°
61°
n=51
r=.51 p<.001


E.
N
50°
68
n=51
r=.41 p<.001
F.
N
50°
n=60
r=.15 p>.20

Of the 3 Piper's beach stock tests, #113A (fig. 13d) and #113B (fig. 13e) were performed under a 3/4 visible moon and both had highly significant mean bearings of 61°N and 68°N respectively, which were not significantly different from the seaward Y-axis direction of 50°N (C.I. tests $p > .05$). The third test (#109A) was random ($p > .20$) (table 12, fig. 13f). These results suggest that the moon does not affect Y-axis orientation.

To determine if the moon influences the orientation strength, the r-values of the tests were compared to the r-values of the clear night tests performed in the absence of a moon (Chapter IV). Since the largest r-value in the moon-present tests (.55) was greater than the largest value in the moonless tests (.46), this suggests that the orientation strength did not degrade in the presence of the moon.

From these results I conclude that generally the crabs are capable of nighttime seaward Y-axis orientation under a partially overcast sky in the presence of the moon, although in some instances directional choices were random. It does not appear that the moon significantly altered the directional preference, since in most significant tests the mean bearings were not significantly different from the Y-axis directions, nor the orientation strength of the crabs.

5) Effect of crab activity level on the directional preference.

To determine if directional preferences were related to activity levels of the crabs, crabs were analysed with respect to 1) the mean length of time to make a trap choice after release and 2) the percentage of crabs tested which did not make a trap choice (% "no choice") (table 13).

Percentage "no choice" levels were significantly higher at sunrise (test #117) and sunset (test #115) as compared to morning, afternoon, and mid-night times. Mean choice times were significantly higher from sunset

Table 13: Effect of activity levels on the directional preference of H. nudus from the P.B.S beach (Y-axis = 150°N) tested at different times of the diel cycle. Mean bearings are in °N.

test		mean bearing	% "no choice"	mean choice time (s)
#	condition			
114	mid-afternoon	163	3.2	7.4
115	sunset	106	20.0	11.8
116	mid-night	187	2.2	11.8
117	sunrise	157	36.2	13.4
118	mid-morning	93	10.8	9.3

through the night to sunrise, than during the day (Chi-squared test $p < .001$) (table 13, fig. 14). This suggests that the level of activity varied during the diel cycle.

The mean choice time and % "no choice" from each test were correlated to the mean bearings, which were transformed from circular to linear data by taking the angular difference of the mean bearing minus the Y-axis direction. These values were then used in the correlation with the other linear variables.

The difference between mean bearings and Y-axis directions were not significantly correlated with mean choice time ($p > .20$) and % "no choice" ($p > .20$), suggesting that changes in activity leves did not affect the directional preference of the crabs.

6) Observer effects.

The effect of the position of the observer during testing and the compass direction of loading the crabs into the release ring on the platform were analyzed with respect to the directional choice.

The analysis was carried out with tests #114-#118 and 12 previous daytime and nighttime experiments which showed significant directional preferences. The effect of the observer position was analyzed by comparing the difference between the Y-axis direction and the crabs' mean bearing, and the difference between the position of the observer and the Y-axis direction (fig. 15). Effect of the direction of loading the crabs into the release ring in the arena was analyzed in the same manner (fig. 16). No obvious changes in mean bearing in relation to the observer's position or loading direction were evident.

b) Factors affecting crab activity levels.

In the previous section, it was discovered that significant differences

Figure 14. Effect of crab activity level on the directional preference of H. nudus from the P.B.S. beach (Y-axis = 150°N) tested at different times of the diel cycle. The circles represent % "no choice", and triangles indicate the mean choice time.

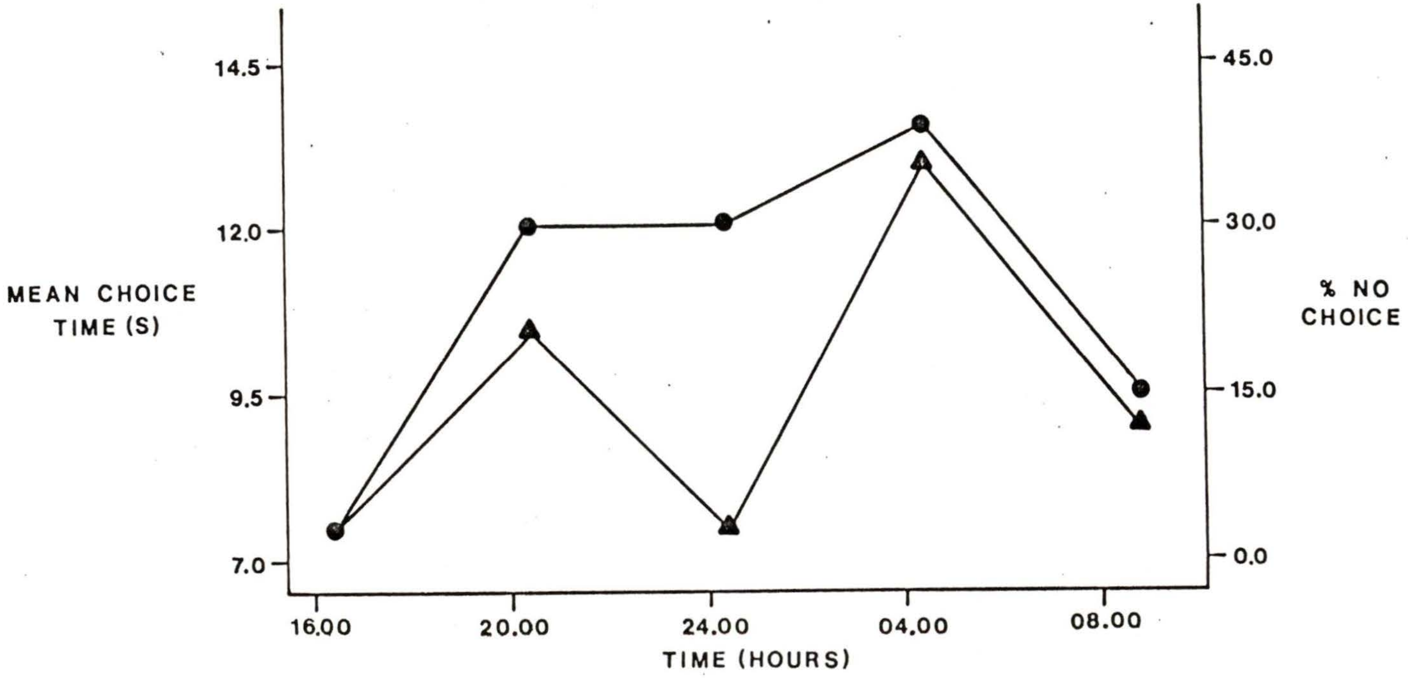

MEAN CHOICE TIME (S)
14.5
12.0
9.5
7.0
% NO CHOICE
45.0
30.0
15.0
0.0
16.00
20.00
24.00
04.00
08.00
TIME (HOURS)

Figure 15. Effect of the observer's position on the directional preference of the crabs. Small dots represent 1 test, large dots represent 2 tests.

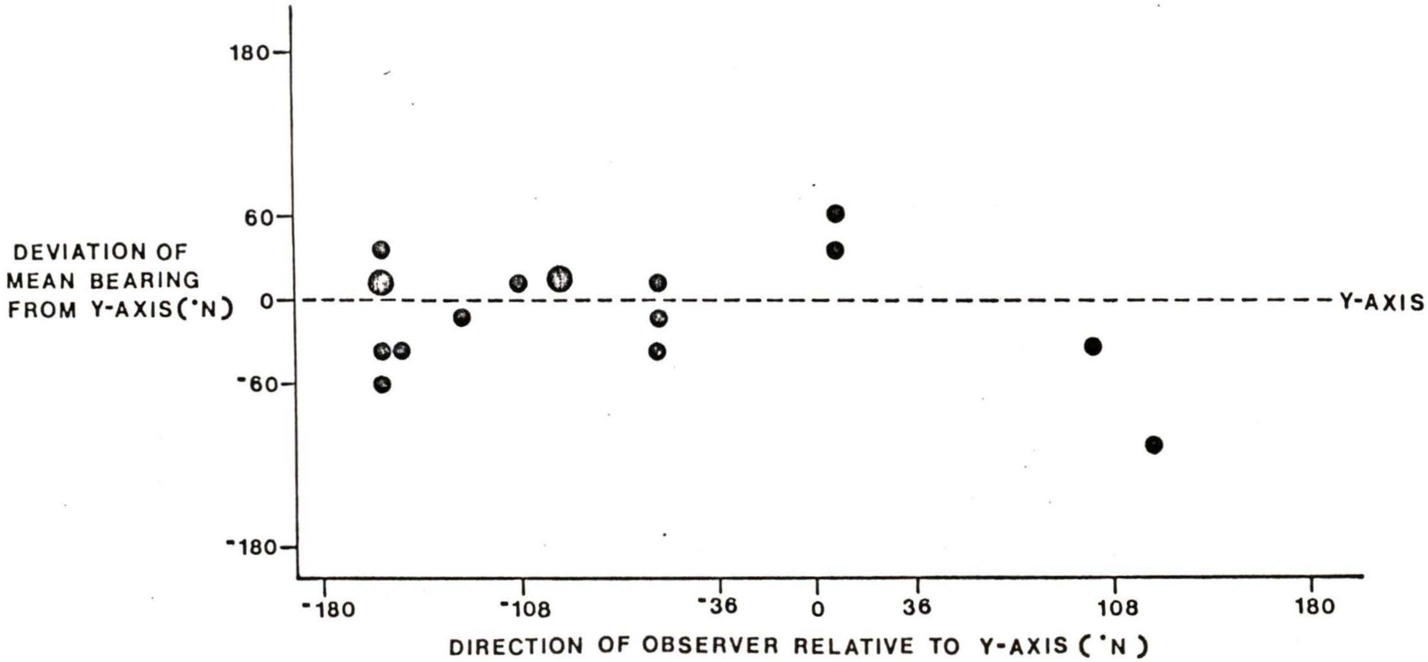
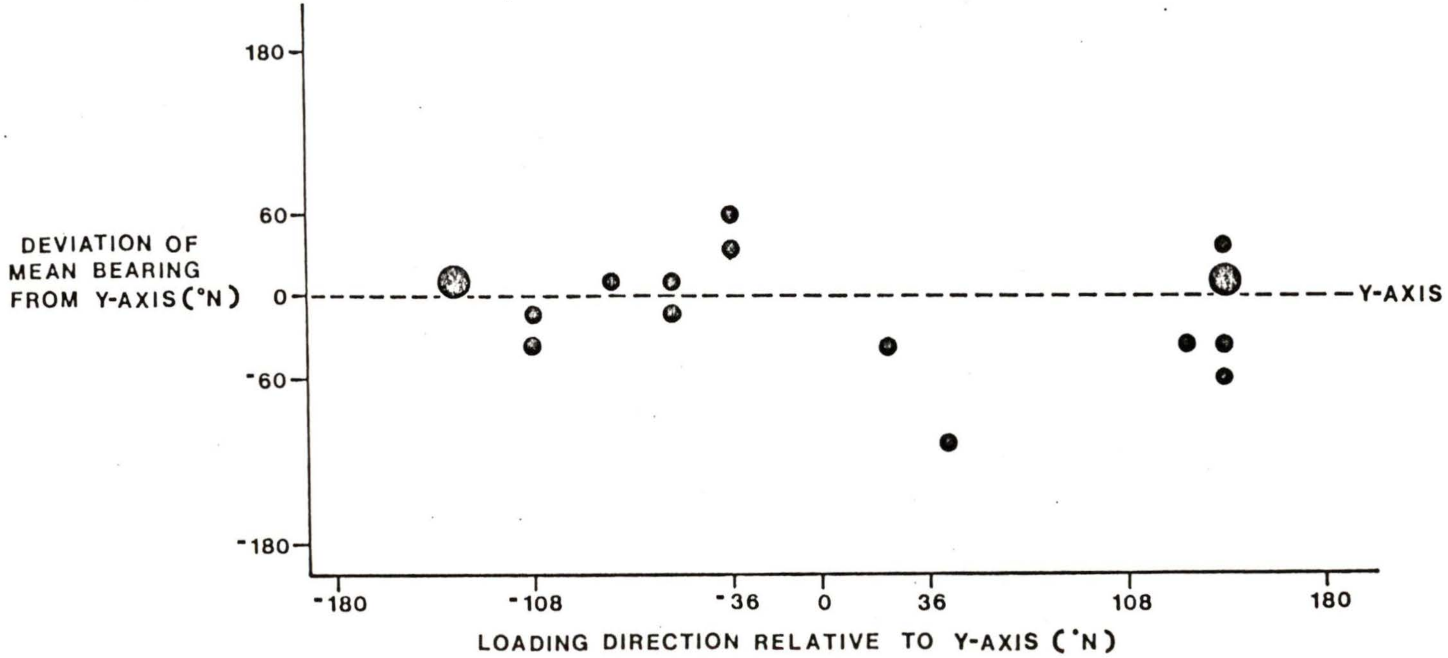

180
60
0
-60
-180
DEVIATION OF MEAN BEARING FROM Y-AXIS (°N)
Y-AXIS
-180
-108
-36
0
36
108
180
DIRECTION OF OBSERVER RELATIVE TO Y-AXIS (°N)

Figure 16. Effect of the direction of loading the crabs into the release ring in the arena on the directional preference. Legend as in fig. 15.


180
60
0
-60
-180
DEVIATION OF MEAN BEARING FROM Y-AXIS (°N)
Y-AXIS
-180
-108
-36
0
36
108
180
LOADING DIRECTION RELATIVE TO Y-AXIS (°N)

in the % "no choice" and mean choice time occurred during different times of the diel cycle, but that these did not affect the mean bearing or orientation strength.

The mean choice time and % "no choice" were not significantly correlated (p> .10) to each other, suggesting that they were independent. They were expected to be dependent since with increasing time to make a trap choice, more crabs are expected to remain on the platform after the 30 s time allotment and will be scored as a "no choice". However, the results suggest that their choice to remain on the platform is independent of the choice to pursue a bearing.

To investigate possible tidal influences on crab activity, the mean choice time and % "no choice" values in table 13 were compared with the 2 tidal parameters in table 11. Neither mean choice time nor % "no choice" were significantly correlated to the tide height (p> .10 and p> .20, respectively) or period of the tidal cycle (p> .20), suggesting that crab readiness to act is not affected by tidal factors.

The 2 crab response measurements in table 13 were compared to test temperatures in table 10. Temperature and mean choice time were negatively linearly correlated (p< .01), but the % "no choice" was not significantly correlated to temperature (p> .20). Thus increases in temperature decreased the mean choice time proportionately. Even though correlation does not necessarily imply causation, I believe these results are evidence that temperature affects crab behavior with respect to travel speed in the testing arena.

CONCLUDING REMARKS

Since the mean bearings and strength of orientation were not affected by the time of day, tides, temperature, crab motivation, the moon, or the observer, it is concluded that the significant fluctuations in mean bearing were most likely due to a random drift about the seaward Y-axis direction. This random drift may be explained by varying individual responses to environmental cues, which would account for the group variance in mean bearings. For example, Adler and Taylor (1981) found that American toads, _Bufo americanus_, show a significant variability in individual responses when performing Y-axis orientation.

A decrease in temperature caused a decrease in activity (time required to make a trap choice). Crabs are poikilothermic and are thus expected to slow down their metabolic rate with lower temperatures. However, temperature was not correlated with the % "no choice", suggesting that the increase in % "no choice" at certain times of the day was not a result of this factor.

The activity decrease based on the % "no choice" observed at sunrise and sunset was most likely due to changing sky conditions. In the sunrise tests, testing started before sunrise and ended before the sun was visible on the horizon. During this period, the moon and stars fade, and eventually disappeared from view. The light intensity and sky color also change during this time. Crabs may be restricted from relying on sky cues during these conditions. Ferguson (1967, 1971) and Ferguson et al. (1965) similarly noted that various species of amphibians fail to orient in the late evening during the period between sunset and the appearance of stars.

Test results with and without the moon at night indicated that the presence of the moon does not affect the orientation. However, Y-axis orientation by use of moon is a common ability of shore-dwelling species. It has been discovered in Fowler's toads, _Bufo fowlerii_ (Ferguson and Landreth, 1966), Southern cricket frogs, _Acris gryllus_ (Ferguson et al., 1965), intertidal amphipods, _Talitrus saltator_ (Papi, 1960; Papi and Pardi, 1963) and _Orchestoidea corniculata_ (Enright, 1961), and the isopod _Tylos latreilli_ (Pardi, 1954). It is not known if _H. nudus_ also posseses an optional lunar orientation capability.

Fluctuations in the orientation ability at night with or without the moon have been noted in other work with intertidal crustacean species. For example, Enright (1972) found that *Talitrid amphipods*, when tested under the moon and stars, sometimes failed to orient. When the animals were significantly directed, the directions were not always along the expected Y-axis, and in some cases the orientation was time compensating for the movement of the moon while in others fixed-angle orientation was observed.

In closing, I conclude that testing Y-axis orientation of *H. nudus* can be performed irrespective of the tidal and diel cycles, and within the range of other parameters under which they were tested. However, in order to minimize the length of a testing period, the tests should not be performed during the changing sky conditions of sunrise and sunset or during low air temperatures.

VI. SKY BLOCKAGE EXPERIMENTS

INTRODUCTION

In the previous section I presented information that H. nudus were able to perform a seaward Y-axis orientation both during the day and night, under relatively clear skies (0-50% overcast). The objective of these experiments was to determine if the clear sky contains important cues by conducting orientation experiments during overcast sky conditions and with the arena artificially covered. If the sky provided the only directional cues, then the crabs should not be able to orient under cover.

Tests were performed with crabs from the P.B.S. beach in Nanaimo (Y-axis = 150°N), and from two shorelines in Barkley Sound; namely Bamfield Church beach (Y-axis = 305°N), and Bamfield Marine Station (B.M.S.) beach (Y-axis = 295°N).

RESULTS

a) Tests performed under heavily overcast skies.

1) Tests performed under daytime overcast skies.

Bamfield Church beach crabs (Y-axis = 305°N) were tested in 6 releases between 1330h - 1600h on July 14, 1982, under partially overcast skies in which the sun was visible only as a faint disc through a completely overcast sky, and in 10 releases under 100% overcast skies. Crabs were tested in groups of 20 in orientation arena #1. They were given 5 min in the ring and 2 min to make a trap choice after release. The results are presented in table 14.

Table 14: Results of daytime overcast trials with the Church beach stock (Y-axis = 305°N). Y-axis (seaward) and mean bearings are in °N, F-value is based on Hotellings one sample test (second-order analysis), and p = probability.

% overcast	# of releases	# of crabs tested	Y-axis	mean bearing	F-value	p
partial	6	118	305	323	2.79	> .10
100%	10	184	305	302	2.93	> .10
pooled	16	302	305	311	4.65	< .05

Table 15: Nighttime 90-100% overcast sky tests with the P.B.S. beach stock (Y-axis = 150°N). n = sample size, Y-axis (seaward) and mean bearings are in °N, and p = probability.

Test #	% overcast	n	Y-axis	mean bearing	r-value	p
111	90-100%	60	150	40	.25	< .05
104	100%	60	150	331	.31	< .005
108A	100%	54	150	355	.15	> .20
108B	100%	53	150	327	.11	> .20
pooled 100%		167	150	343	.18	< .005

Both tests with Church beach crabs produced mean bearings close to the seaward Y-axis direction, but the directional preferences were not significantly different from uniformity (p> .10) (table 14, fig. 17a,b).

The tests did not have statistically different mean bearings (Watson-Williams analysis p> .25), and crabs in both of the tests had a similar orientation strength (F-value) (table 14). When pooled, the tests produced a statistically significant mean bearing of 311°N (p< .05), which was close to the seaward Y-axis direction of 305°N (fig. 17c). The pooled results suggest that some type of directional cue for Y-axis orientation is available during partially and totally overcast skies. However, since the strength of the orientation was weaker than that in the clear sky tests (Chapter IV), this indicates that daytime clear sky orientation cues are important for Y-axis orientation.

2) Tests performed under nighttime overcast skies.

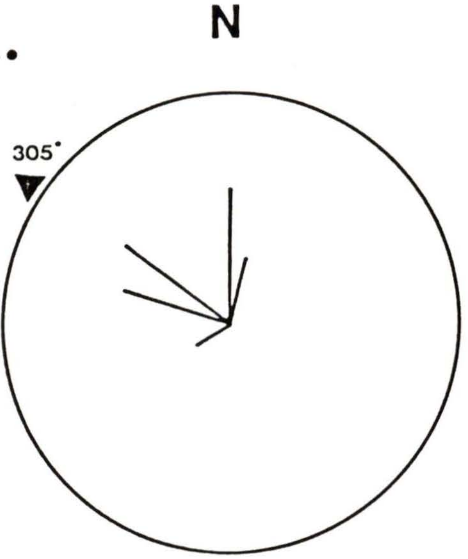
Nighttime testing under overcast skies consisted of 4 experiments with the P.B.S. beach stock (Y-axis = 150°N) done between 2239h - 0345h on June 19 - July 6, 1984. Crabs were tested singly in arena #2 and the support table was used. The crabs were given 30 s in the ring and 30 s to make a trap choice after release. The results are presented in table 15.

Test #111 performed under a 90-100% overcast had a mean bearing of 40°N (p< .05) (table 15, fig. 18a). This direction was 110° counterclockwise of the expected direction, or half-way between the seaward Y-axis direction of 150°N and the 330°N landward Y-axis direction.

The next 3 tests (#104, #108A, and #108B) performed under a 100% overcast sky had mean bearings of 331°N, 355°N, and 327°N respectively, which were close to 180° opposite the seaward Y-axis direction, along the landward Y-axis direction of 330°N (table 15, fig. 18b-d). However,

Figure 17. Results of daytime overcast trials with the Church beach stock (Y-axis = 305°N); (a): partially overcast, (b): 100% overcast, and (c) pooled results of a,b. Legend as in fig. 4.

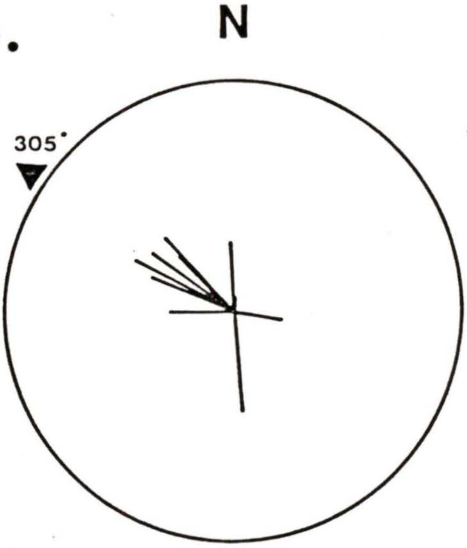
A.



n=6

F=2.79 p>.10

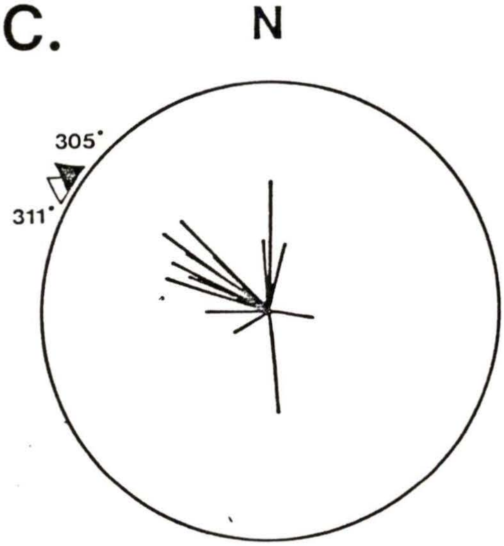
B.



n=10

F=2.93 p>.10

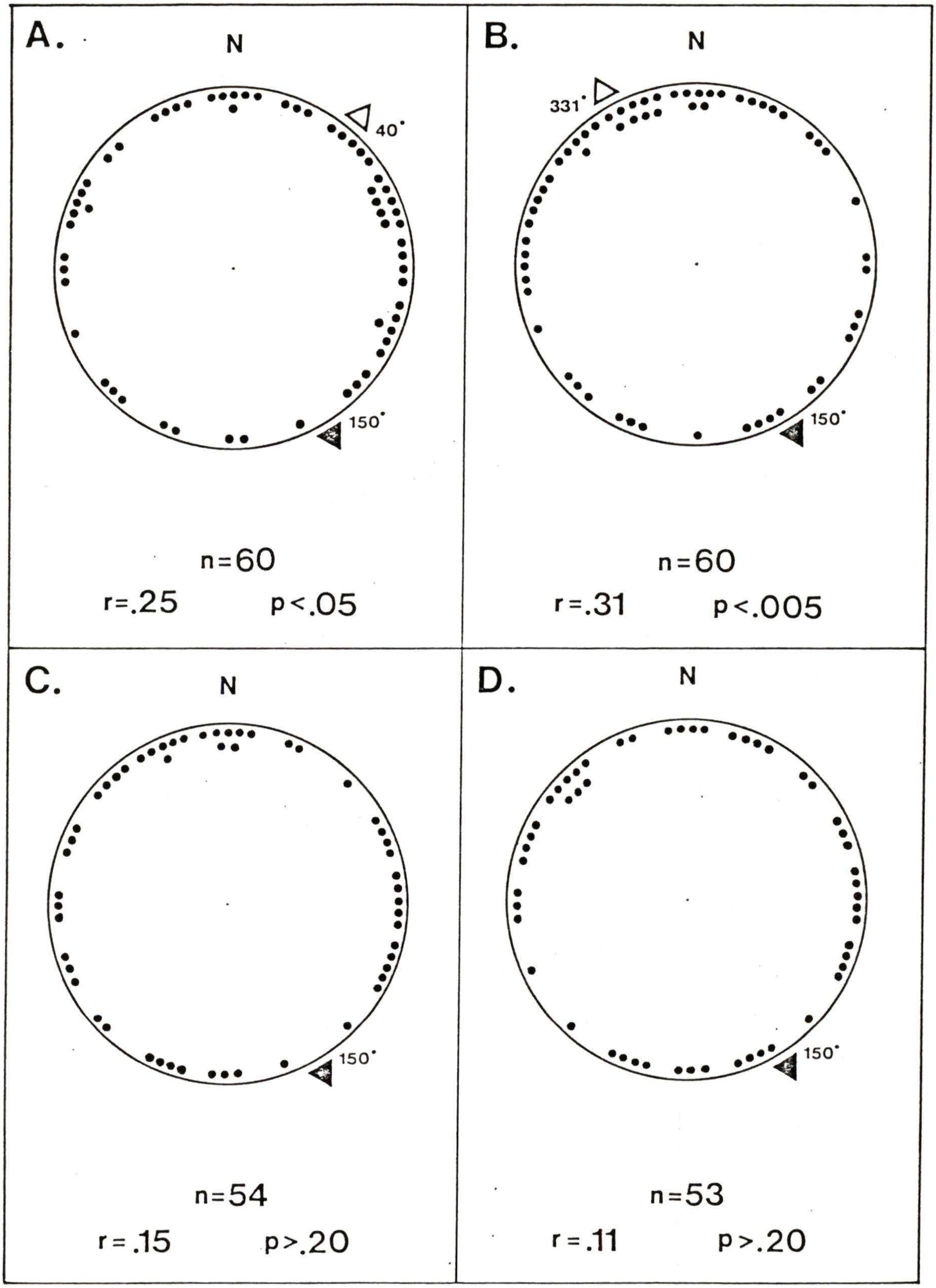
C.

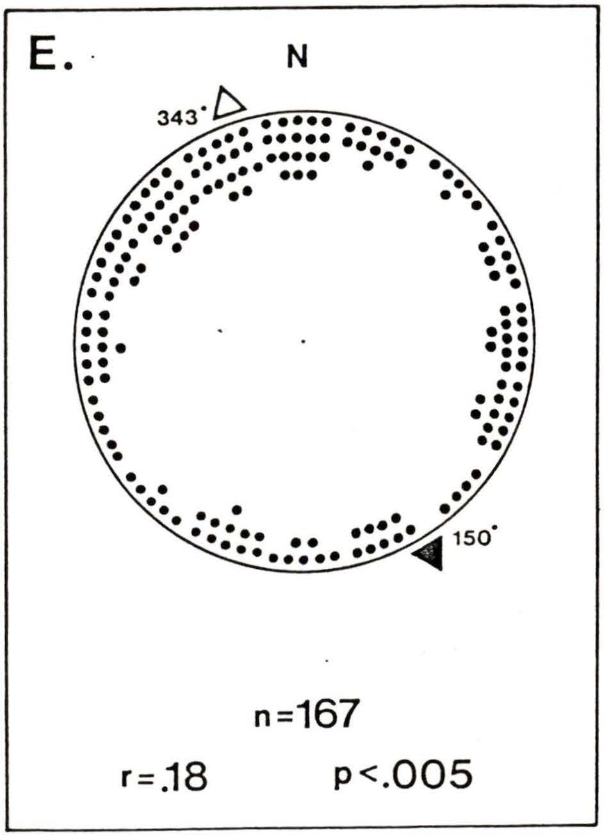


n=16

F=4.65 p<.05

Figure 18. Nighttime 90-100% overcast sky tests with the P.B.S. beach stock (Y-axis = 150°N); (a): Test #111, 90-100% overcast, (b-d) Tests #104, #108A, & #108B, with 100% overcast, (e) pooled data. Legend as in fig. 6.


A.
N
40°
150°
n=60
r=.25 p<.05
B.
N
331°
150°
n=60
r=.31 p<.005
C.
N
150°
n=54
r=.15 p>.20
D.
N
150°
n=53
r=.11 p>.20


E.
N
343°
150°
n=167
r=.18
p<.005

the results were not statistically significant in all cases and only test #104 had a significant mean bearing of 331°N, which was in the landward Y-axis direction (C.I. test $p > .05$). When these tests were pooled, the results of the 3 tests produced a significant mean bearing of 343°N, which was in the landward Y-axis direction of 330°N (C.I. test $p > .05$) (table 15, fig. 18e).

These results indicate that under heavily overcast night skies (90% - 100%), the mean bearing switches to a landward Y-axis direction and that the directional choices become less directed.

b) Tests performed under cover.

1) Tests performed under cover in daylight.

For these experiments, a wooden cage was placed around the orientation arena and support table. A cover of white opaque sheeting on the upper half and translucent white sheeting on the bottom half was positioned over the cage, blocking a view of the sky, but allowing depolarized daylight to enter. A detailed description of this testing apparatus can be found in the section on magnetic orientation. The cover was removed from the cage for the control test.

Five experiments were performed with the P.B.S. beach stock (Y-axis = 150°N) between 1150h - 1744h on Sept. 1-17, 1984. Crabs were tested singly in orientation arena #2, including the support table, and given 30 s in the ring and 30 s to make a trap choice after release. The results are presented in table 16.

Test #138 was conducted as a control experiment with no cover on the cage. Orientation was strong and directed seawards, however the mean bearing of 105°N was significantly different from the seaward Y-axis direction of 150°N (C.I. test $p < .01$) (table 16, fig. 19a).

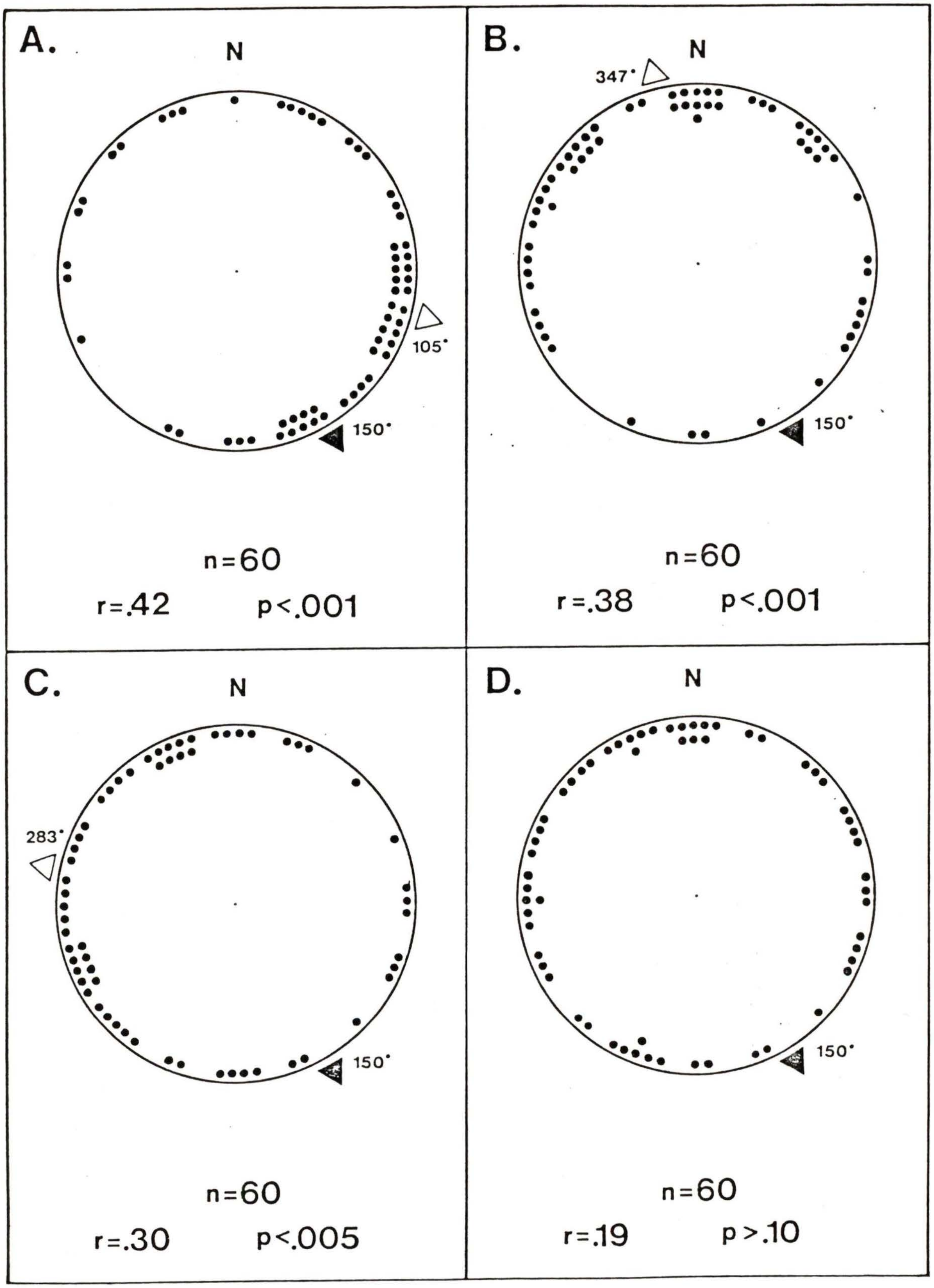
Table 16: Results of covered and uncovered tests performed in daylight with the P.B.S. beach stock (Y-axis = 150°N). n = sample size, Y-axis (seaward) and mean bearings are in °N, and p = probability.

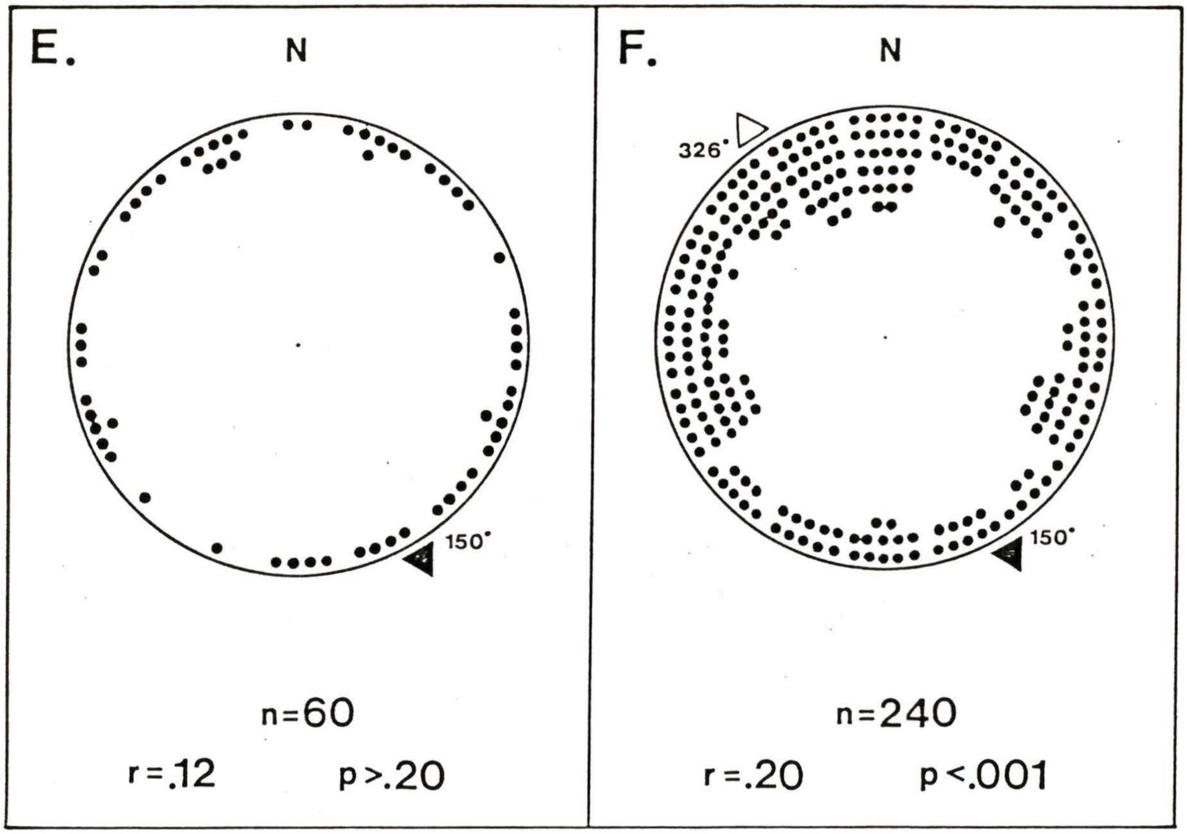
test #	test condition	% overcast	n	Y-axis	mean bearing	r-value	p
138	uncovered	45	60	150	105	.42	< .001
126	covered	30	60	150	347	.38	< .001
128	covered	100	60	150	283	.30	< .005
130	covered	50	60	150	325	.19	> .10
132	covered	70	60	150	142 & 322	.12	> .20
pooled covered			240	150	326	.20	< .001

Table 17: Results of tests performed under cover in total darkness with the B.M.S. beach stock (Y-axis = 295°N). Y-axis (seaward) and mean bearings are in °N, F-value is derived from Hotellings one sample test, and p = probability.

# of releases	# of crabs tested	Y-axis	mean bearing	F-value	p
8	154	295	270	0.73	> .25
5	87	295	224	0.09	> .25
8	150	295	223	0.10	> .25
pooled	231	295	243	0.10	> .25

Figure 19. Results of covered and uncovered tests performed in daylight with the P.B.S. beach stock (Y-axis = 150°N); (a): Test #138, uncovered control test, (b-e): Tests #126, #128, #130, & #132 conducted under cover, (f) pooled data of b-e. Legend as in fig. 6.


A.
N
105°
150°
n=60
r=.42 p<.001
B.
N
347°
150°
n=60
r=.38 p<.001
C.
N
283°
150°
n=60
r=.30 p<.005
D.
N
150°
n=60
r=.19 p>.10


E.
N
150°
n=60
r=.12
p>.20
F.
N
326°
150°
n=240
r=.20
p<.001

Covered tests #126 and #128, with mean bearings of 347°N and 283°N were significantly different from uniformity (table 16, fig. 19b,c). However, only in test #126 was the mean bearing significantly close to the landward Y-axis direction (C.I. test $p > .05$), while in test #128 it was not (C.I. test $p < .05$). Even though Tests #130 and #132 (fig. 19d,e) did not produce significant results due to small r-values, the mean bearing of 325°N in test #130 was very close to the landward Y-axis direction and the bimodal mean bearings of 142°N and 322°N in test #132 were close to the landward and seaward Y-axis directions of 150°N and 330°N.

The strength of the orientation in the most significant covered test (#126) (fig. 19b) was not significantly different from that of the uncovered test (#138) (fig. 19a) (r-value test $p > .25$), suggesting that the orientation can be as directed under cover as under the unobstructed blue sky. When all covered tests were pooled, a mean bearing of 326°N ($p < .001$) was in the landward Y-axis direction of 330°N (C.I. test $p > .05$) (fig. 19f).

These results indicate that without a view of the sky, purple shore crabs tend to orient in a landward Y-axis direction, similar as under overcast skies. Also, orientation without a view of the sky is opposite to and sometimes less directed than under clear sky conditions. These results also suggest that orientation cues other than those provided by the daytime sky must have been used.

2) Tests performed under cover in total darkness.

Tests in total darkness were done inside the main laboratory at B.M.S. between 0500h - 2330h on July 12-14, 1982. Crabs from the B.M.S. beach (Y-axis = 295°N) were tested in 21 releases in groups of 20 in orientation arena #1. A lightproof cardboard lid, painted flat black, was placed over the arena to test the crabs in complete darkness. The crabs were given 5 min in the ring and 2 min to make a trap choice after release. The results are presented in table 17.

Crabs in the 3 tests had no significant directional preferences (p> .25) (table 17, fig. 20a-c). Pooling the vectors of all samples resulted in a distribution which was not significantly different from uniformity (p> .25) (fig. 20d). This indicates that total darkness without a view of the sky, the orientation ability of the crabs is hampered.

CONCLUDING REMARKS

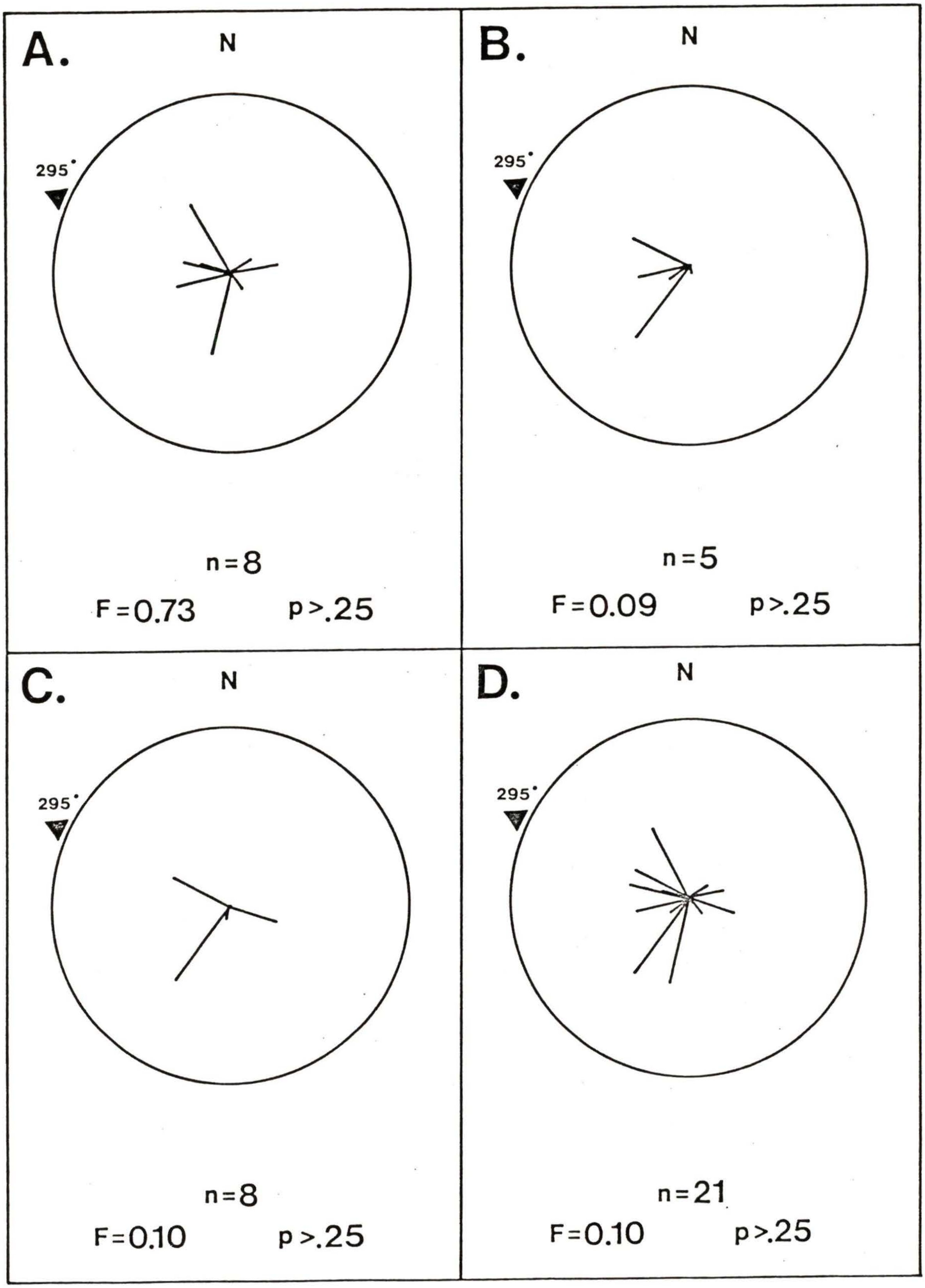
The objective of the series of tests under overcast skies and under cover was to determine if the clear sky contains important cues for orientation.

No directional preference was shown by crabs tested in complete darkness. Yet the crabs were able to orient under completely overcast night skies and under cover when tested in daylight. Assuming that the crabs tested at night oriented by the use of non-visual cues, these 2 results suggest that orientation is blocked in complete darkness. Thus one factor affecting orientation appears to be the light intensity.

The orientation was along the general seaward Y-axis under completely overcast skies, but was less directed than under clear skies (Chapter IV). This suggests that the clear sky contains important information for orientation. In contrast, under a completely overcast night sky, the orientation direction changed 180° counterclockwise to a general landward Y-axis direction. These two results further suggest that the reversed orientation at night is an effect of light intensity.

The reversed orientation to a landward Y-axis direction was also observed in daytime tests conducted under cover. The 180° shift was not likely caused by decreased light intensity under the cover in this case. Support for this conclusion is that the crabs in the diel effect tests (Chapter V) were found to orient in the seaward Y-axis direction during dusk and dawn. During these times, the light intensity was less

Figure 20. Results of tests performed under cover in total darkness with the B.M.S. beach stock (Y-axis = 295°N); (a-c): tests conducted in total darkness, (d): pooled data of a-c. Legend as in fig. 4.


A.
N
295°
n=8
F=0.73
p>.25
B.
N
295°
n=5
F=0.09
p>.25
C.
N
295°
n=8
F=0.10
p>.25
D.
N
295°
n=21
F=0.10
p>.25

than that of these tests conducted under cover. Rather, I propose that the complete blockage of the view of the sky was responsible for the reversal of the orientation direction in the daytime covered tests. Sky cover appears to be a second factor affecting the orientation response, and suggests that view of the clear sky provides important directional information for orientation.

The crabs in one daytime test under cover (#132) were bimodally oriented along the Y-axis. Although the results were not statistically significant, the mean bearings are in the general landward and seaward Y-axis directions. A switch to bimodal orientation under cover is not uncommon. For example, Groot (1965) and Quinn and Brannon (1982) observed a change from a unimodal orientation to a bimodal one along one orientation axis in sockey salmon, Onchorhynchus nerka, when their testing tanks were covered. Bingman (1981) similarly observed a bimodal orientation in savannah sparrows tested under cover. The bimodal orientation in my results may represent some intermediate condition between normal and completely reversed orientation, in which the directional choice of the crabs was divided in the two Y-axis directions.

Why the landward Y-axis orientation takes place is presently not known. It may indicate a switch to a different orientation system, such as one based on non-visual cues, when light intensity (night overcast tests) and/or view of the sky (daytime covered tests) are markedly reduced.

Relative humidity is a factor responsible for reversed orientation along the Y-axis in the beach-dwelling Talitrus saltator, and also for the reversed orientation direction in Tenebrio molitor (Arendse, 1978). It is however unlikely that H. nudus switched their orientation to a landward Y-axis direction due to the increased relative humidity during these periods for the following reasons. The reversed orientation persisted even in test #126 conducted under cover during 30% overcast, hot and sunny sky conditions with low relative humidity, and in control test #138 conducted without the cover, the crabs oriented in the seaward direction.

Part 3. Analysis of directional cues used in Y-axis orientation.

VII. ANALYSIS OF DIRECTIONAL CUES USED IN Y-AXIS ORIENTATION.

INTRODUCTION

The previous tests demonstrated that a view of the clear sky is important for seaward Y-axis orientation, since in most instances orientation deteriorated in crabs tested under heavily overcast skies or under cover.

The sun and polarized light pattern of the sky are two obvious visual cues during daylight, as are stars and the moon during the night. A diversity of species orienting solely by visual cues such as the sun, fail to do so under complete cloud cover. Some examples are amphipods (Papi, 1960), crabs (Herrnkind, 1968; Nishimoto and Herrnkind, 1982), fish (Goodyear and Ferguson, 1969; Hasler et al., 1958; Winn et al., 1964), amphibians (Dole, 1972; Ferguson, 1963, 1967; Ferguson and Landreth, 1966; Ferguson et al., 1968; Jordan et al., 1968; Landreth and Ferguson, 1967a, 1967b; Goodyear, 1970), reptiles (Murphy, 1981), and birds (Kramer, 1952; Sauer, 1957).

Sometimes orientation persisted under cover or under heavy overcast, suggesting that the crabs may also use non-visual cues for orientation. Past research on non-visual orientation has primarily focussed on the use of geomagnetic cues. Weak radiation (Brown Jr., 1963; Brown et al., 1962) and electrostatic fields (Webb et al., 1961) apparently also provide directional information for snails. An interdependance of these 2 types of cues with other factors such as the earth's magnetic field and time of day greatly complicates research in these fields. In this chapter, I will present information on the importance of visual directional cues in section VIIa and of non-visual directional cues in section VIIb.

a) Visual directional cues.

1. MIRROR EXPERIMENTS

INTRODUCTION

The purpose of these experiments was to determine whether H. nudus are able to utilize orientation cues provided by the daytime sky by subjecting the crabs to horizontally displaced mirror images of the sky. Four large mirrors were used to deflect 4 areas of the sky either 90° clockwise or counterclockwise. One of the 4 reflections contained the sun. It was hypothesized that a corresponding shift in the crabs' orientation would signify that the animals were relying on the sun to provide directional information.

The mirror technique has been successfully used by Kramer (1952) to study sun orientation in starlings (Sturnus vulgaris). Pardi (1954) altered the lunar Y-axis orientation response in the isopod Tylos latreillii by using mirrors to change the position of the moon, and Nishimoto and Herrnkind (1982) demonstrated that blue crabs (Calinectes sapidus) altered their offshore Y-axis orientation when the position of the sun was changed clockwise or counterclockwise from its normal position with mirrors.

EXPERIMENTAL PROCEDURE

Crabs collected from the P.B.S. beach (Y-axis = 150°N) were used in 8 experiments between July 24- Aug. 4, 1984. Testing began within 2 h of capture, during which time the crabs were kept in their collection buckets.

Orientation arena #2 was used and the support table was raised by 42.5 cm to minimize observer interference. A wheel base with 2" casters was attatched to the table legs to facilitate rotation of the entire apparatus. The orientation arena was covered by a plywood box (85 x 85 x

64 cm high) with four windows (fig. 21). Each window was equipped with a set of rails extending past the end of the open side. Mirrors (31 x 41 cm) were inserted in the rails with mirrored sides facing inward and by sliding they could be moved along the rails in front of the windows or out of view behind the box walls. When the mirrors were in front of the windows, blinds were added in order to exclude undeflected side light. The lightproof top of the box was removable for access to the arena. The release ring was suspended from a screw-eye in the rooftop. The box was painted flat white to maximize the light intensity within it and to minimize unwanted reflections.

With the mirrors in place, the crabs on the platform were thus presented with a view of the sky that was rotated 90° clockwise or counterclockwise, depending on which way the mirrors were positioned on the box. The mirrors were moved out of view for the control tests. The box position was changed between tests.

Crabs were introduced into the release ring through one of the windows of the box. They were tested singly and given 30 s in the ring and 30 s to make a trap choice after release. The sun was not visible from within the release ring, but only from certain areas on the platform.

RESULTS

Six experiments were performed between 1230h - 1840h from July 24 to August 4, 1984, consisting of two control tests without the use of mirrors, 2 counterclockwise, and two clockwise altered sky tests. The results are presented in table 18 and fig. 22a-g.

Tests #119 and #123 were control tests performed without the use of mirrors. While test #119 produced a significant mean bearing of 83°N ($p< .001$), test #123 did not (table 18, fig. 22a,b). It can however be seen in fig. 22a that a bimodal orientation exists towards the NE and

Figure 21. Apparatus for altered sky experiments; (1) box apparatus, (2) box lid, (3) mirrors, (4) light deflectors, (5) orientation arena #2, (6) support table.

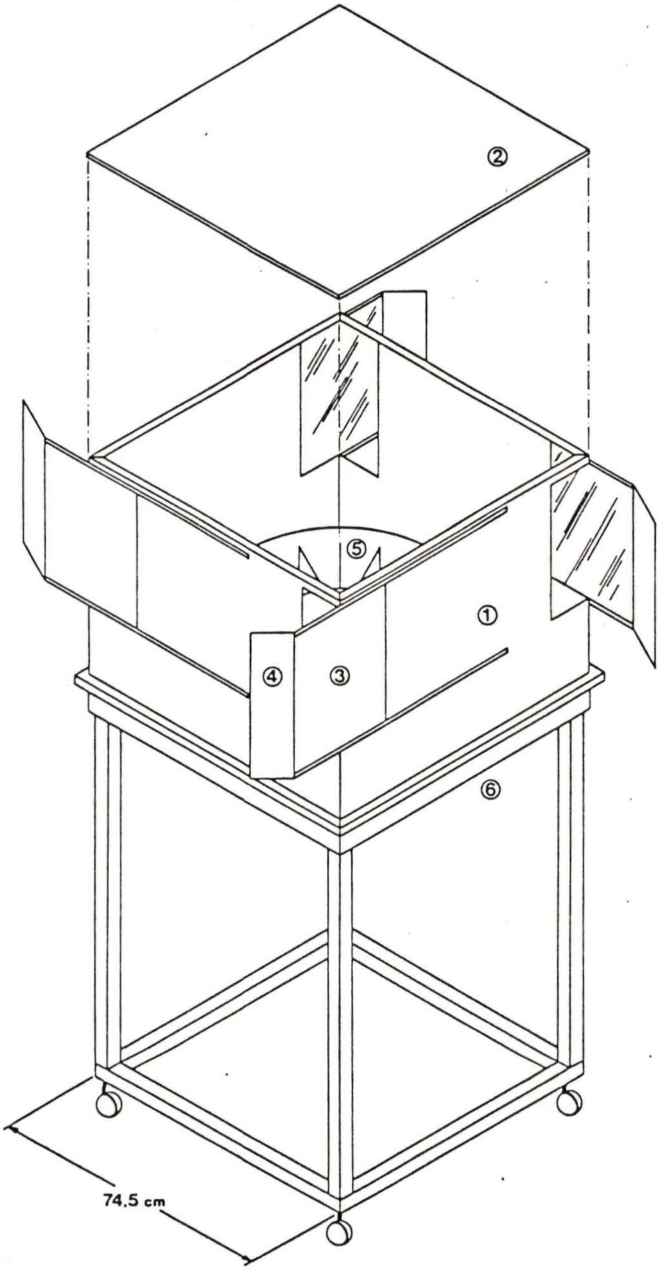
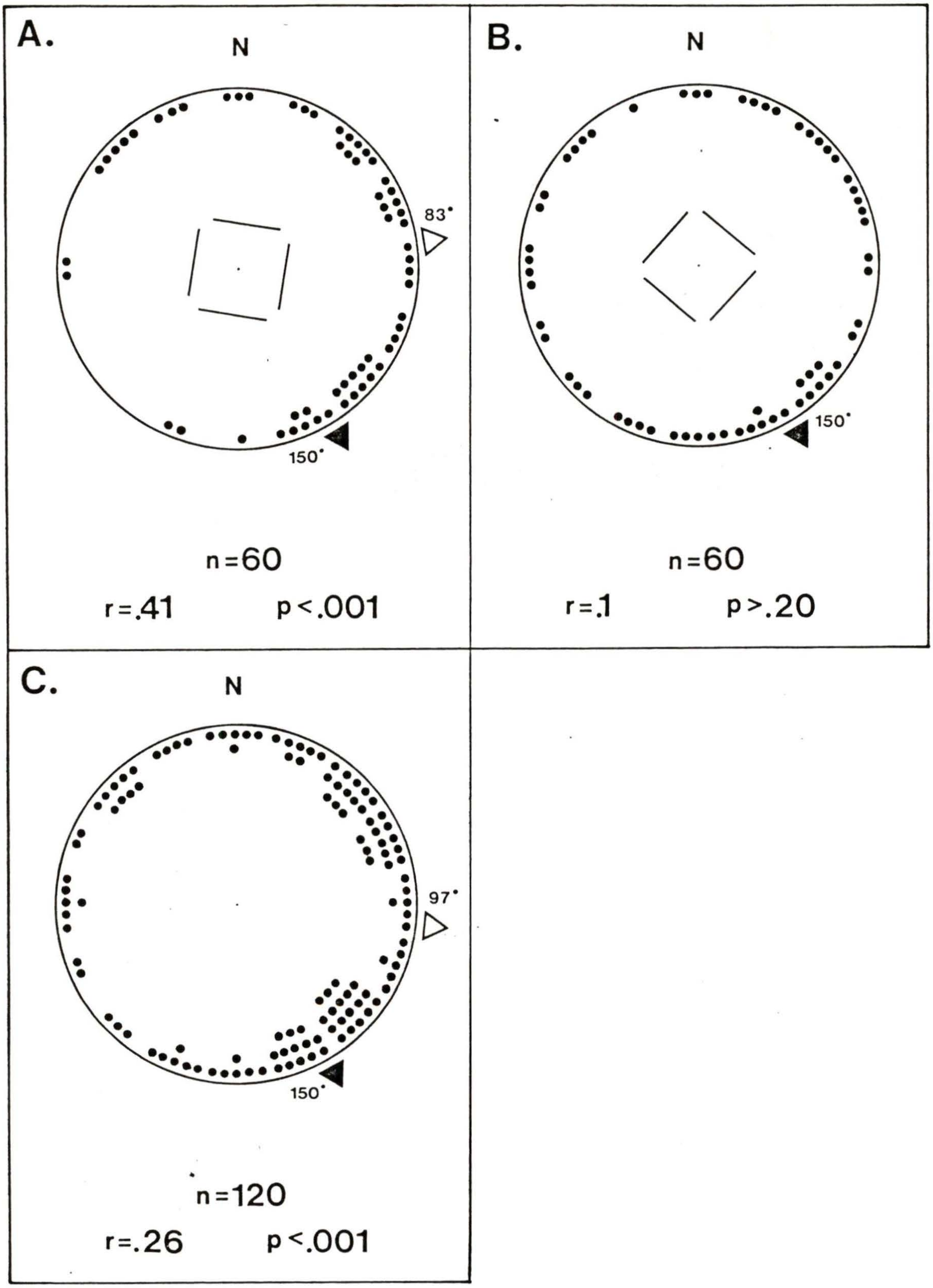
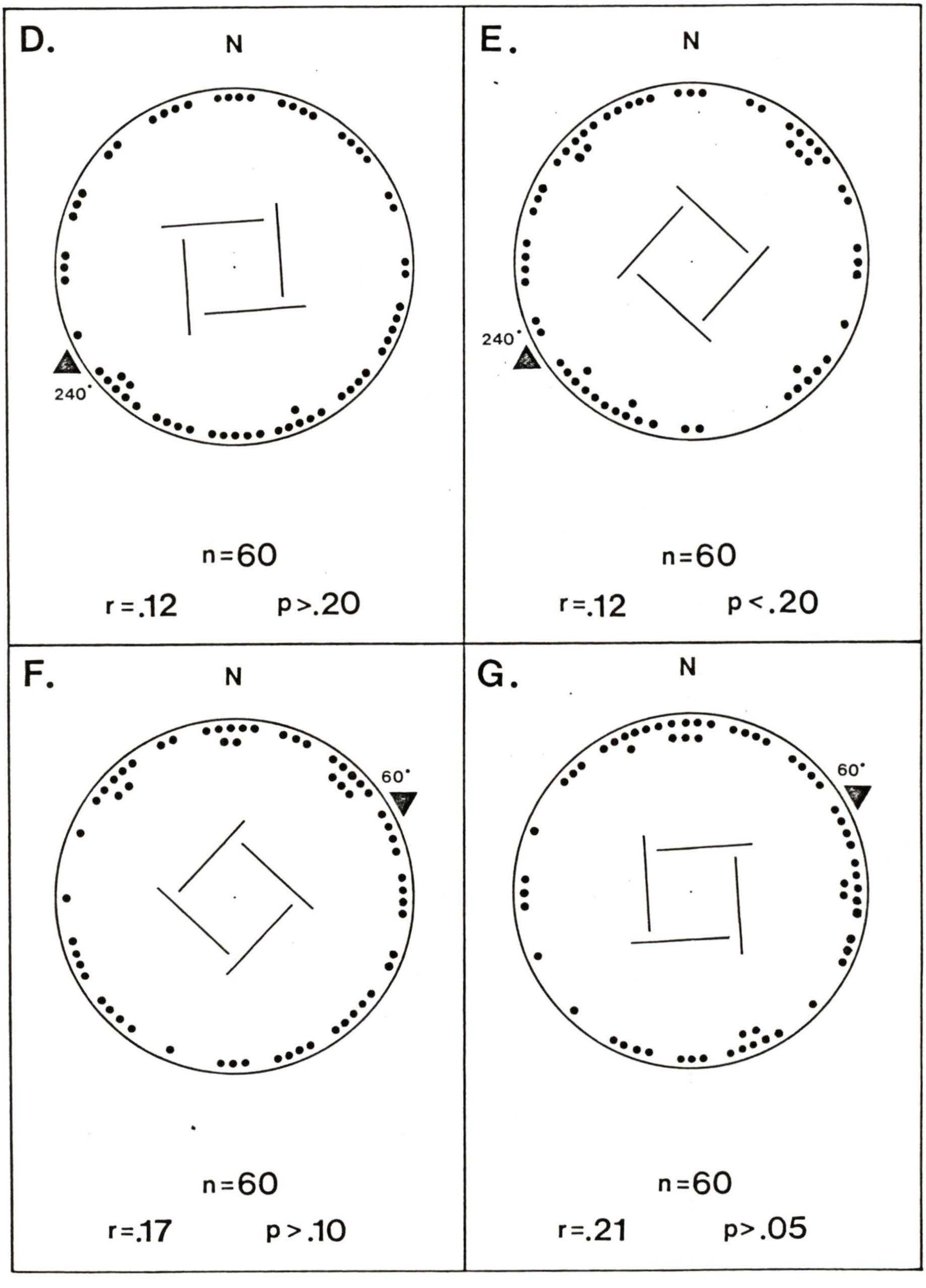

②
⑤
①
④
③
⑥
74.5 cm

Table 18: Results of daytime mirror experiments with the P.B.S. beach stock (Y-axis = 150°N), under relatively clear skies (5-10% overcast). Box position, expected directions, and mean bearings are in °N, n = sample size, and p = probability.

test #	test condition	box position	expected direction	n	% sky overcast	mean bearing	r-value	p
119	control	280	150	60	10	83	.41	< .001
123	control	222	150	60	5	135	.16	> .20
	pooled controls		150	120		97	.26	< .001
121	clock. altered	267	240	60	5	165	.12	> .20
122	clock. altered	222	240	60	5	311	.12	> .20
	pooled clock. altered		240	120	5	242	.04	> .50
124	countercl. altered	222	60	60	10	41	.17	> .10
125	countercl. altered	267	60	60	10	51	.21	> .05
	pooled countercl. altered		60	120	10	46	.19	< .02

Figure 22. Results of altered sky experiments with the P.B.S. beach stock (Y-axis = 150°N), under relatively clear skies (5-10% overcast); (a,b): control tests #119 & #123 without the use of mirrors, (c) pooled results of a,b, (d,e): clockwise altered tests #121 & #122, (f,g): counterclockwise altered tests #124 & #125. Positioning of the box relative to the orientation arena is depicted by the broken square figure. Other legend as in fig. 6.


A.
N
83°
150°
n=60
r=.41
p<.001
B.
N
150°
n=60
r=.1
p>.20
C.
N
97°
150°
n=120
r=.26
p<.001


D.
N
240°
n=60
r=.12
p>.20
E.
N
240°
n=60
r=.12
p<.20
F.
N
60°
n=60
r=.17
p>.10
G.
N
60°
n=60
r=.21
p>.05

SE. Since the two directions are not 180° apart, statistical analysis for bimodality fails. No standard method exists to determine the mean directions and statistical significance of this type of orientation. While the NE direction was not anticipated since it does not correspond to any direction of previous results conducted with this population, the SE direction corresponds to the seaward Y-axis direction of 150°N. These results indicate that the box covering the orientation arena affected the daytime directional preference of the crabs. Test #123 shows the same bimodal orientation direction as test #119 (fig. 22b), and a plot of the pooled data shows the bimodal pattern more clearly (fig. 22c). The mean bearing of 97°N for the pooled results was highly significant ($p < .001$).

Two tests (#121 & #122) were performed with the sky shifted 90° clockwise by use of the mirrors and resulted in random orientation ($p > .20$) (fig. 22d). Pooling the two tests produced a non-significant mean bearing of 242°N ($p > .50$), which was however close to the expected direction of 240°N. The counterclockwise altered tests (#124 & #125) were not significant ($p > .05$), although the mean bearings of 41°N and 51°N were close to those of the expected direction of 60°N based on the shifted sky pattern (fig. 22f,g). Pooling these two tests produced a mean bearing of 46°N ($p < .02$), not significantly different from the expected direction of 60°N (C.I. test $p > .05$).

CONCLUDING REMARKS

The testing apparatus severely interfered with the orientation ability. However, the mean bearings of the two control tests showed a bias toward an easterly direction, approximately in the Y-axis direction of SSE.

Once the mirrors were introduced, crabs showed reduced orientation, most likely as a result of a reduction of the light intensity within the apparatus due to placement of mirrors. Due to the almost perfectly clear skies used for the testing (5-10% overcast), no effect of cloud cover was considered. Mean bearings based on pooled results however did show a bias in the mean bearing towards the expected directions based on the shifted sky pattern.

Possibly the change in the light intensity patterns within the apparatus after the mirrors were added was sufficient to change the orientation from a Y-axis type based on sky cues, to one based on differential light intensity. Orientation based on light intensity differences is a common ability of many intertidal animals such as amphipods, Talitrus saltator (Williamson, 1951).

The box used in these experiments eliminated view of the sky directly overhead, and only allowed the crabs to see the sky up to 30° from horizontal (at the center of the platform). The sun could not be seen from the center of the platform during testing, since it was not sufficiently low in the sky to be reflected onto the platform. This may also have affected the crabs' response. A different, more open, testing apparatus allowing a full view of the sun might have alleviated the problem by providing a more strongly directional light source. It is also possible that a multimodal orientation resulted from the mirrors producing a differential light intensity pattern around the arena.

The results obtained in these experiments were inconclusive and necessitated the use of other testing apparatus to determine if the crabs use orientation cues in clear day and night skies.

2. ARTIFICIAL SUN EXPERIMENTS

INTRODUCTION

Some animals orient to a stationary artificial light source as readily as they would to the real sun, either in a fixed-angle (phototactic) or time-compensated manner. In time-compensated orientation, when the artificial light source is held stationary, the animals' orientation direction shifts a predicted average of 15°/h, as they compensate for the normal 15°/h average sun azimuth movement. In fixed-angle phototactic orientation to the sun, the animals orient at a set angle to the moving sun. This method of using an artificial sun has been sucessfully used with a variety of animals such as mosquitofish (Gambusia affinis) (Goodyear and Ferguson, 1969), bluegill sunfish (Lepomis macrochirus) (Hasler et al., 1958), and Fowler's toads (Bufo woodhousei fowleri) (Landreth and Ferguson, 1968).

Artificial sun experiments with H. nudus were carried out under controlled laboratory conditions. The crabs were tested over approximately a 6 h period each day. It was hypothesized that if the crabs used sun cues in time-compensated sun-compass orientation and regarded the artificial sun as being real, then their orientation direction should shift approximately 15°/h with respect to the artificial sun's position.

EXPERIMENTAL PROCEDURE

Crabs were collected from the Rocky Point beach (Y-axis = 330°N) and were transported to the test facility by car in the plastic collection buckets with lids. They were stored for less than 14 h prior to testing in the holding tanks (previously described) at the Pacific Biological Station. The animals were tested in 12 experiments between 0910h - 1730h from Oct.11 to Nov.3, 1984.

The experiments were carried out inside a small laboratory room (about 4 x 4 m) at the Pacific Biological Station. The windows of the room were covered with black plastic, eliminating visual outdoor cues such as the sun and polarized light. Orientation arena #2 and support table were used.

The artificial sun apparatus consisted of a 14" polished aluminum reflector mounted on an adjustable tripod. A 500 W Sylvania EBW B2 Superflood color-corrected incandescent bulb (GTE Products Corp., Salem, Mass.) was used as the artificial sun. This bulb has a color temperature of about 4800° Kelvin, the same as early afternoon and late morning daylight (Eastman Kodak Co., 1977). Thus the color balance of light from the artificial sun was close to that of the real sun at those times of the day. The light intensity was monitored with a Vivitar 45 light meter (Vivitar Canada Ltd., Vancouver) and was set close to the ambient light intensity outdoors with a fully visible sun.

All distances on the apparatus were set with respect to the desired light intensity, angle of the sun, and heat generated by the bulb relative to the platform of the orientation arena. The light bulb was always positioned at a direct-line distance of 180 cm, measured from the center of the platform to the filament of the bulb. The temperature on the platform was 20-25°C, about 5°C higher than the ambient room temperature.

Four sets of experiments were performed. Each set consisted of 3 tests run in succession so as to span a period of 6-7 h in total. A short break was taken between consecutive tests.

The first set of experiments were performed with the artificial sun positioned in the E (90°N), and with the elevation angle of the bulb set at 31°, corresponding to the azimuth and elevation of the real sun at the start of the test. The artificial sun remained at that position for the remaining 2 tests in the series, even though the real sun elevation and azimuth changes over the course of the day. It was assumed that the elevation of the light source was not as critical as the azimuth. For example, Landreth and Ferguson (1968) found no affect on the sun-compass orientation of Fowler's toads (Bufo woodhousei fowleri), even when the elevation of their artificial sun was decreased from 51° to a position just visible on the horizon of the test arena.

The second set of 3 tests was conducted in exactly the same manner, but with the sun at 31° elevation in the N (360°N), while the third set of tests was conducted with the sun at zenith at the same direct-line distance from the platform as in the previous tests. A fourth set of tests were performed with the sun again positioned in the East. However, this time the orientation arena was flooded with sea water to a depth of 2.0 cm on the platform, so that the test crabs would be fully submerged. This set of tests served as a comparison for the first set of dry tests in which the sun was also in the E and to determine if a difference in response could be elicited from crabs by using this technique.

The artificial sun was turned on about 10 min prior to each testing period. The lab room was lightproof, with all other light sources sealed off. Each crab was given 30 s in the ring and 30 s to make a trap choice after release. Animals to be tested were held out of direct path of the light source in the lab in white plastic buckets with lids.

RESULTS

The results are presented in table 19 and figs. 24-27. The expected directions of travel were calculated from the median time of each test duration. One average expected direction of travel was assigned to each test, based on the 15°/h sun azimuth movement, even though the tests took longer than 1 h to complete.

Tests #159-#161 were performed with the sun positioned at zenith for control purposes. Centering the light at zenith produced an equal light

Table 19: Results of artificial sun experiments with the Rocky Point (Y-axis = 330°N) stock. Expected direction and mean bearings are in °N, n = sample size, and p = probability. Only the most highly significant mean bearigs are presented for clarity.

test #	test condition	median test time (hm)	expected direction	n
153	sun in E (at 90°N)	0957	330	60
154		1328	277	60
155		1600	239	60
156	sun in N (at 360°N)	1002	240	60
157		1240	200	60
158		1542	155	60
159	sun at zenith	1138	none	60
160		1409	none	60
161		1645	none	60
178	sun in E (at 90°N)-underwater	1013	330	60
179		1235	294	60
180		1459	258	60

test #	unimodal mean bearing	r-value	p	bimodal mean bearing	r-value	p
153	67	.33	< .002	0 & 180	.28	< .01
154	112	.26	< .02	10 & 190	.23	< .05
155	145	.33	< .002	2 & 182	.21	> .05
156	354	.17	> .10	91 & 271	.26	< .02
157	8	.20	> .05	91 & 271	.23	< .05
158	334	.17	> .10	98 & 278	.47	< .001
159	57	.19	> .10	90 & 270	.08	> .50
160	60	.25	< .05	31 & 211	.11	> .20
161	270	.17	> .10	99 & 279	.05	> .50
178	223	.10	> .50	176 & 356	.38	< .001
179	273	.15	> .20	171 & 351	.35	< .001
180	164	.19	> .10	184 & 4	.61	< .001

intensity distribution in the different directions of the arena. It was assumed that if the crabs were showing some sort of phototactic behavior, as seemed to be evident from the responses to the light source in prior experiments with the view of the clear sky obstructed (Chapters VI, VIII), then they should orient randomly due to the lack of differential light intensity within the arena. No expected direction of travel was established since it was not known how the crabs would respond in this situation. Tests #159 and #161 showed random orientation ($p > .10$), but test #160 had a significant unimodal bearing of 60°N ($p < .05$) (fig. 25a-c).

Tests #153-155 were performed with the artificial sun in the east. In the first test, the expected direction of travel was in the seaward Y-axis direction of the home beach (330°N), and in the following 2 tests 277°N and 239°N, respectively, based on the position of the artificial sun source.

All 3 tests produced significant unimodal mean bearings determined to be statistically different from each other (Watson-Williams analysis $p < .001$) (table 19, fig. 23a-c). The changes in mean bearings between successive tests were perfectly negatively correlated ($r = -1.0000$, $p < .001$) with the changes of the expected directions among successive tests. This correlation indicates that the mean direction shifted approximately 15°/h, as would be expected if the crabs were using the sun as an orientation cue, but the shift was clockwise rather than counterclockwise, as was expected if the crabs were responding to the position of the sun.

Even though the unimodal results in the 3 tests were highly significant, bimodal analyses were performed since bimodal orientation was observed in some of the later tests in this series. Although the bimodal results were less significant than the unimodal ones, a clear bimodal directional preference in all 3 tests was shown towards the N and S, directly perpendicular to the position of the sun in the east. All 3 tests produced similar mean bimodal directions, which were not

Figure 23. Results of artificial sun experiments with the Rocky Point (Y-axis = 330°N) stock, with the sun positioned in the E (90°N); (a): Test #153, median time of test 0957h, (b): Test #154, 1328h, (c): Test #155, 1600h. Star shape represents position of the sun relative to the arena. Other legend as in fig. 6.

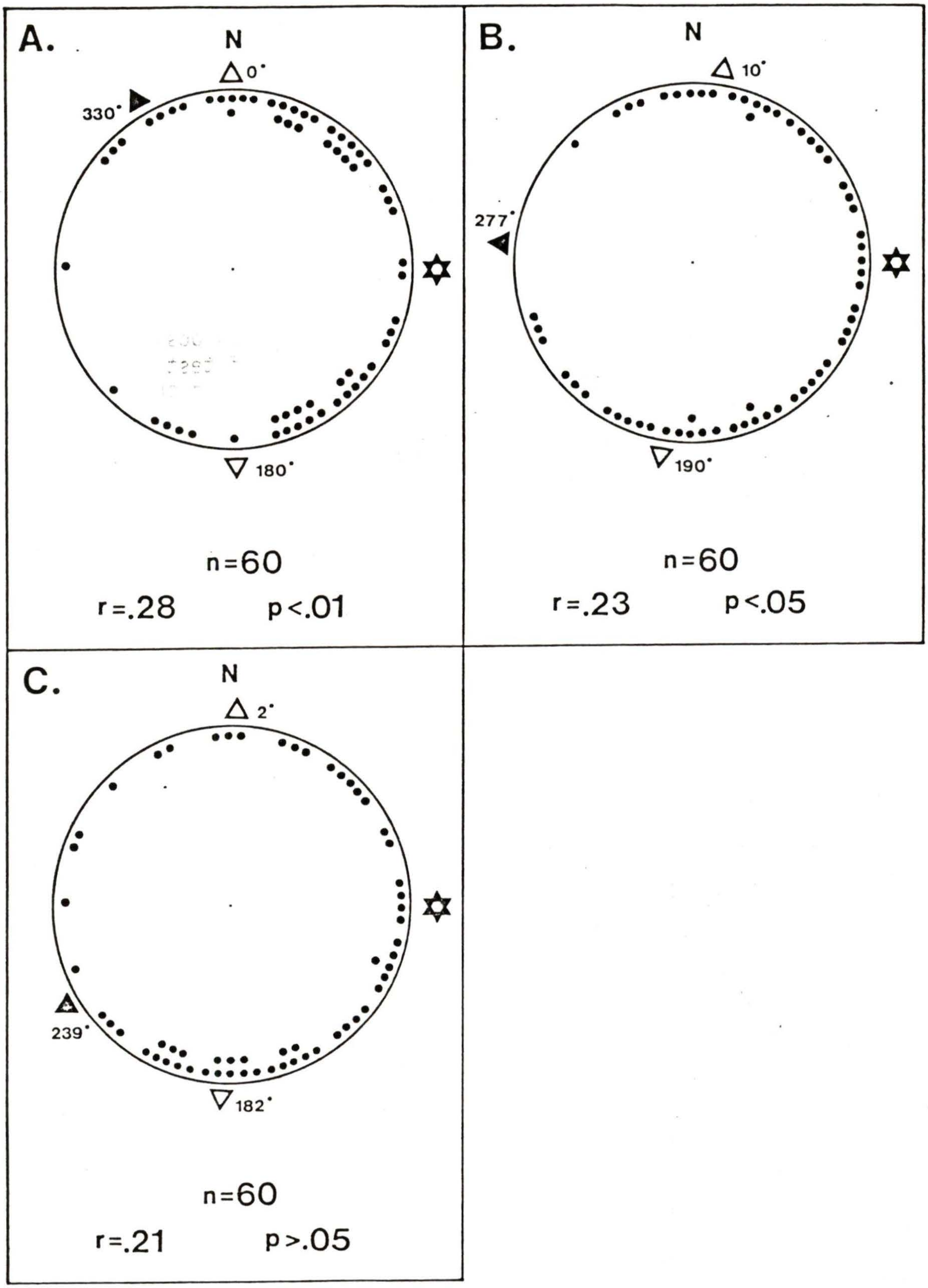

A.
N
0°
330°
180°
n=60
r=.28
p<.01
B.
N
10°
277°
190°
n=60
r=.23
p<.05
C.
N
2°
239°
182°
n=60
r=.21
p>.05

Figure 24. Results of artificial sun experiments with the Rocky Point (Y-axis = 330°N) stock. Sun was positioned in the N (360°N). (a): Test #156, median time of test 1002h, (b): Test #157, 1240h, (c): Test #158, 1542h. Legend as in fig. 23.

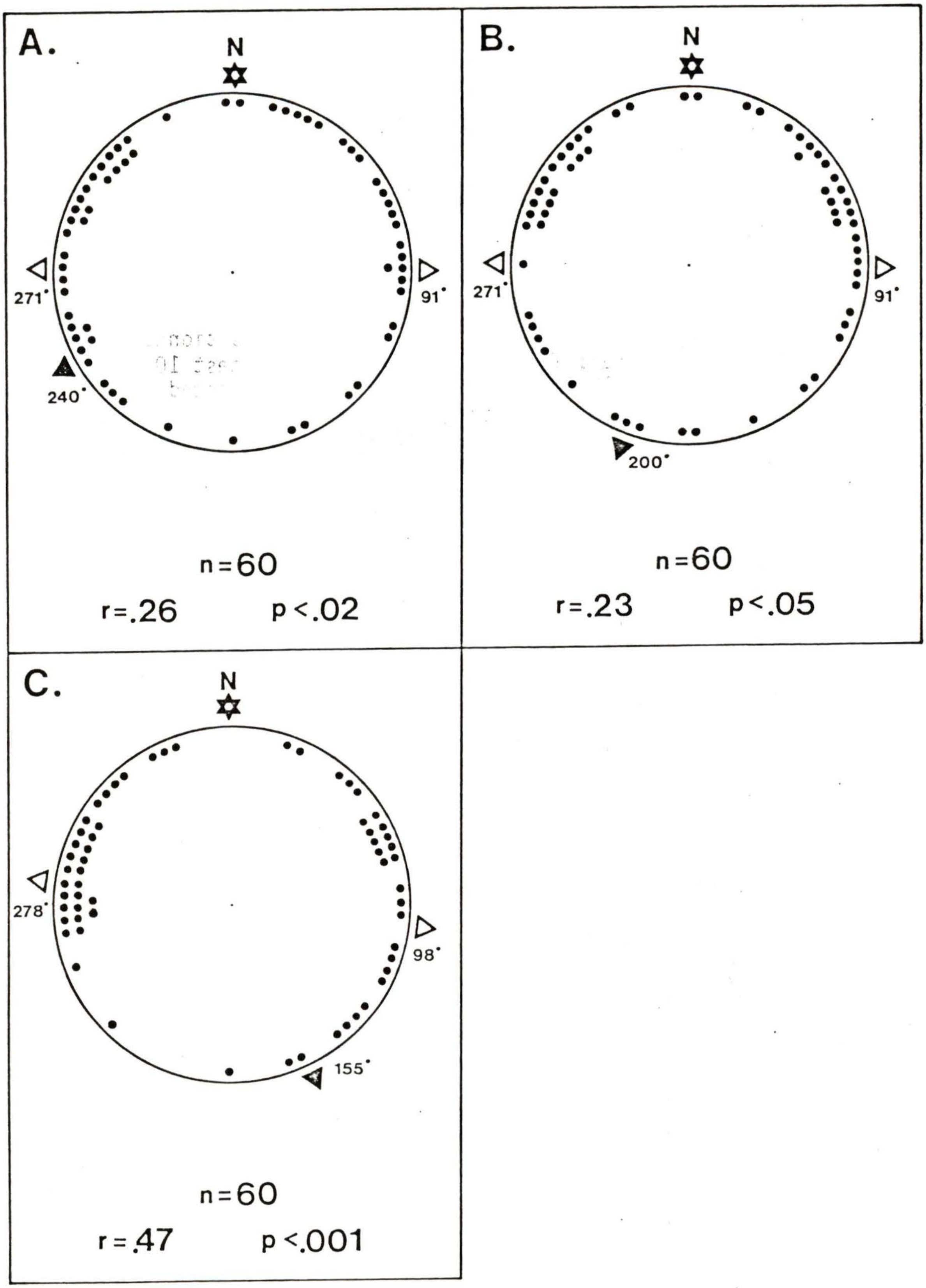
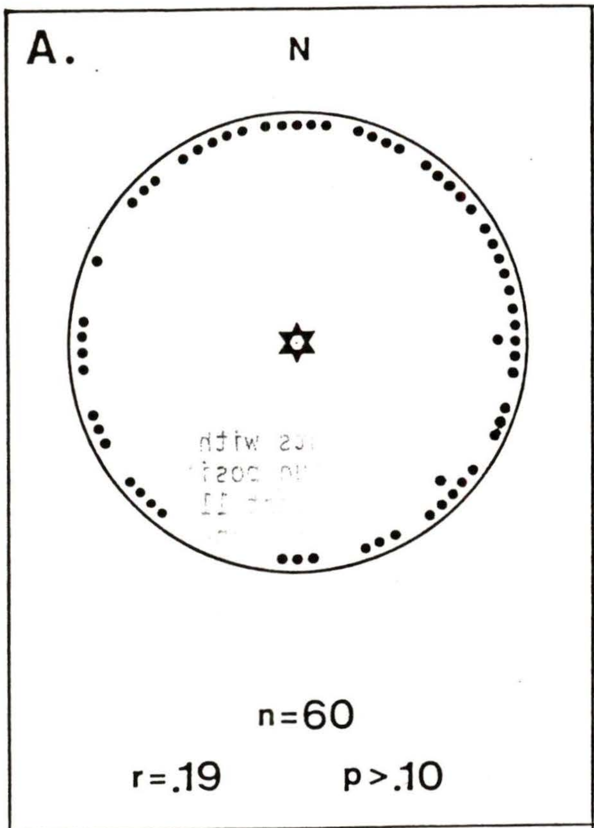
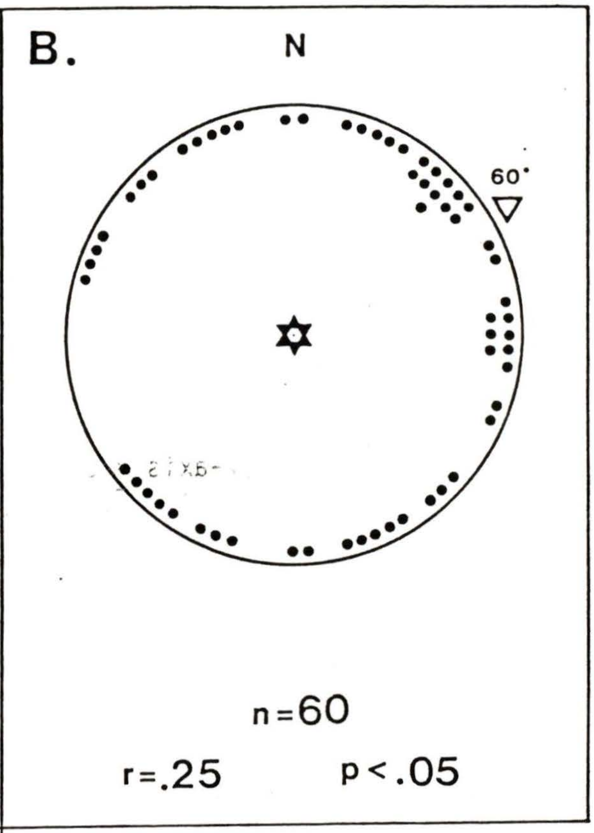

A.
N
271°
91°
240°
n=60
r=.26
p<.02
B.
N
271°
91°
200°
n=60
r=.23
p<.05
C.
N
278°
98°
155°
n=60
r=.47
p<.001

Figure 25. Results of artificial sun experiments with the Rocky Point (Y-axis = 330°N) stock, with the sun positioned at the zenith. (a): Test #159, median time of test 1138h, (b): Test #160, 1409h, (c): Test #161, 1645h. No expected direction of travel was established since no directional preference was expected to a zenithal sun. Other legend as in fig. 23.

A.



B.



C.

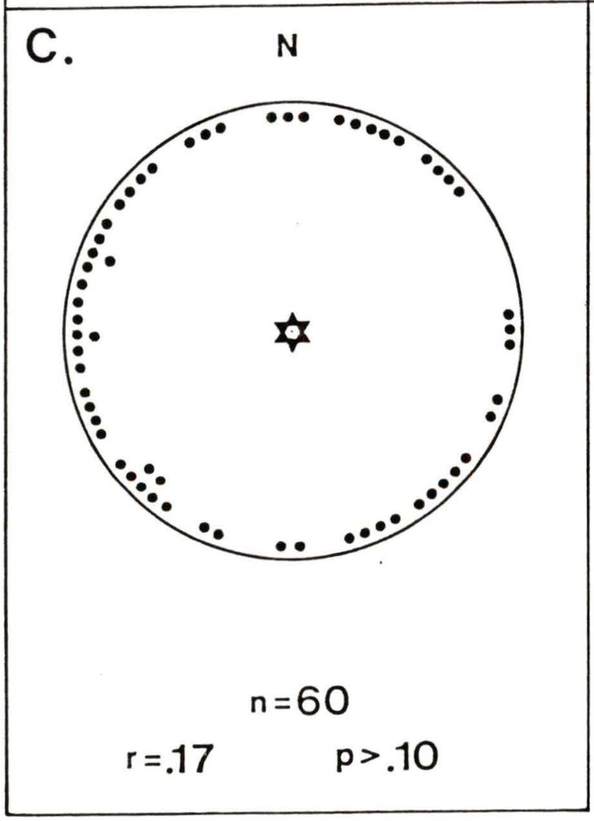
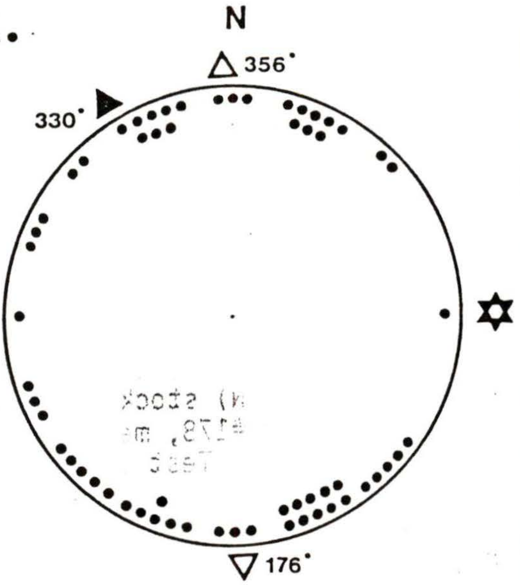


Figure 26. Results of artificial sun experiments conducted underwater with the Rocky Point (Y-axis = 330°N) stock. The sun was positioned in the E (90°N); (a): Test #178, median time of test 1013h, (b): Test #179, 1235h, (c): Test #180, 1459h. Legend as in fig. 23.

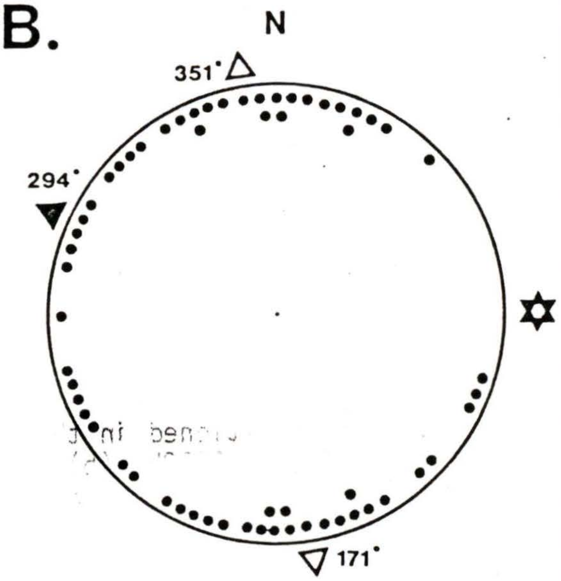
A.



n=60

r=.38 p<.001

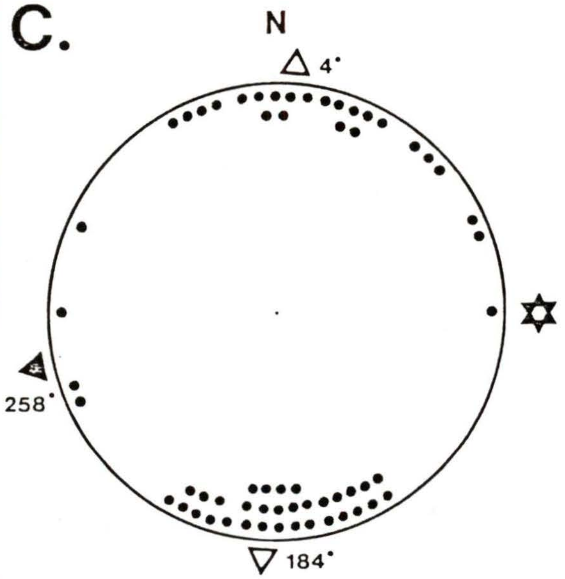
B.



n=60

r=.35 p<.001

C.



n=60

r=.61 p<.001

statistically different from each other (Watson-Williams analysis p> .25). It is likely that the unimodal mean directions were only an artifact. When the figures (fig. 23a-c) are examined, it can be seen that a bimodal N and S orientation occurs, but the apparent bias either in the N or S orientation preference by individuals in any one test produced the nonsense unimodal mean directions. Thus the crabs were orienting in some phototactic manner with respect to the position of the artificial sun.

Tests #156-158 were performed with the artificial sun positioned in the N. All 3 tests produced significant bimodal orientation to the E and W, which was directly perpendicular to the position of the sun in the N (fig. 24a-c). The bimodal directions were not statistically different from each other (Watson-Williams analysis p> .25). These results also indicate that the orientation was phototactic with respect to the position of the sun.

To determine if the observed bimodal orientation was due to effects of heat or decreased humidity resulting from the floodlamp, tests were performed underwater with the sun once again positioned in the east. The water acted as a heat filter and eliminated possible humidity effects. The 3 tests showed highly significant (p< .001) bimodal orientation with modes in N and S, at right angles to the position of the artificial sun (fig. 26a-c). The bimodal directions were not statistically different from each other (Watson-Williams analysis p> .10). These results indicate that heat or humidity factors did not affect the orientation direction and that the response was phototactic.

CONCLUDING REMARKS

The crabs did not respond to the artificial sun in a time-compensated manner. Results from the tests performed with the sun in the N and those underwater with the sun in the E made it clear that the crabs were orienting at right angles to the direction of the light source. Light intensity measurements in the orientation arena showed that the light intensity was lowest by those traps which were positioned perpendicular to the light source. As an example, with the artificial sun in the N, light falling on the platform from the north was reflected from the white concave inside of the arena on the S side, just above the traps. This reflected light was focussed towards the opposite side, in the direction of the light source in the N. Thus the lightest parts of the arena were the N and S sides. Consequently, the darkest areas of the arena were in the W and E. The crabs thus travelled to the darkest areas of the arena. From this I conclude that H. nudus were negatively phototactic in the artificial sun experiments.

Artificially induced phototactic responses have been noted in other species when tested for orientation indoors under an artificial light source without a view of the sky or real sun. For example, sockeye salmon smolts, Onchorhynchus nerka, show a positive phototactic response (Simpson, 1979). Schone and Braemer (1963) tested mangrove crabs, Goniopsis cruentata, for a Y-axis response to polarized light cues from an artificial sun. All individuals were negatively phototactic. Crabs subjected only to polarized light from a diffuse light source, with no artificial sun present, oriented with respect to the polarized light in the expected Y-axis direction. This demonstrated that the presence of an artificial sun seriously interfered with the other directional cue that the crabs were able to use. The artificial light source in my experiments may have affected the directional preference of H. nudus in a similar manner.

Why a negative phototactic response was not evident in crabs tested under the real sun is not known at this time. For example, the Rocky Point crabs in the initial outdoor tests travelled to 330°N, the seaward Y-axis direction. Since the real sun would always lie on the southern side of the orientation arena during testing, the crabs travelled into the lightest parts of the arena in the northern hemicircle. Obviously other cues are more important for orientation than are light intensity differences in outdoor testing.

In contrast, many successful orientation tests using an incandescent artificial sun light source similar to the one used in these experiments have been carried out. In all instances, the researchers used ordinary non-color-corrected incandescent light bulbs of various light intensities. For example, Landreth and Ferguson (1968) successfully used normal, non-color-corrected 25°W and 750°W incandescent bulbs in testing sun-compass orientation of Fowler's toads (*Bufo woodhousei fowleri*), while Goodyear and Ferguson (1969) succeeded in testing Y-axis sun-compass orientation of mosquitofish (*Gambusia affinis*) with similar 275°W and 300°W bulbs. It was the success of these tests which prompted me to use an artificial sun, and from their results it seems probable that the quality of the artificial sun in my experiments was not responsible for the lack of the Y-axis orientation response.

3. POLARIZED LIGHT EXPERIMENTS

INTRODUCTION

The purpose of these experiments was to determine if H. nudus are capable of using orientation cues provided by sky polarization (polarotaxis). The capacity of Crustacea to perceive polarized light was first discovered in Daphnia sp. (Pardi and Papi, 1961). Polarized light sensitivity seems to be a common ability in many marine invertebrate taxonomic groups such as in the Copepoda, Mysidacea, Isopoda, Amphipoda, Aostracca, and Decapoda.

Polarized light perception in marine decapods has been disovered in the hermit crab (Eupagurus bernhardus) (Kerz, 1950); giant land crab (Cardisoma guanhumi) (Waterman and Horch, 1966); green crab (Carcinus maenas) (Shaw, 1966; Horridge, 1967); ghost crab, (Ocypode quadrata) (Schöne and Schöne, 1961); spider crab (Libinia emarginata) (Eguchi and Waterman, 1968); and horseshoe crab (Limulus polyphemus) (Waterman, 1950). Y-axis orientation to the e-vector of polarized light (plane of polarization) has been demonstrated in the ghost crab (Ocypode ceratopthalma) (Daumer et al., 1963), mangrove crab (Goniopsis cruentata) (Schöne and Braemer, 1963), and the sand fiddler crab (Uca pugilator) (Herrnkind, 1966, 1968).

The e-vector of polarized skylight is the primary parameter for orientation since it is predictable and is the most stable polarized light cue over a wide range of atmospheric conditions. The absolute radiation parameters such as radiance, degree of polarization (up to 10%), and spectral distribution are of minor importance (Brines and Gould, 1982; Rossel and Wehner, 1984).

Polarization of the light reflected from the blue sky is due to a scattering of the sun's rays by molecules of the earth's atmoshphere (Waterman, 1951). The natural polarization pattern in the sky is complex. On the celestial sphere where the sun forms one pole and the anti-sun forms the other, polarization is linear and varies from 0 near the sun and anti-sun, to a maximum at the celestial sphere's equator. At all points on the sphere, the e-vector is perpendicular to the direction of the sun (Waterman 1951).

The greatest amount of light transmited through the polarizer is when the e-vector of the filter is positioned perpendicular to the direction of the sun; i.e. in the same plane as the direction of overhead skylight polarization. Conversely, the least amount of light transmission occurs when the e-vector is placed parallel to the direction of the sun. In this case the ambient polarized skylight is blocked by the e-vector of the polarizer.

Both indoor and outdoor tests were performed, using two different experimental procedures. For the initial outdoor tests and all indoor tests, the polarizer e-vector was lined up along the E-W or N-S axis. The polarizer was not moved with time since I wanted to determine if fixed-angle orientation to the e-vector of polarized light occurs. Fixed-angle orientation to polarized light has been observed in various decapod species such as the ghost crab, Ocypode ceratopthalma (Daumer et al., 1963). It was hypothesized that if fixed-angle orientation to the e-vector did occur, then the orientation direction would remain constant through time.

In other outdoor experiments, a different approach was chosen. The position of the e-vector was set either perpendicular or parallel to the direction of the sun. Time-compensated orientation to the e-vector of skylight polarization is displayed by some decapod species such as mangrove crabs, Goniopsis cruentata (Schöne and Schöne, 1963). Crabs orienting in a time-compensated manner were expected to consistently orient in the expected direction.

APPARATUS

The orientation apparatus is depicted in fig. 27. Orientation arena #2 and the support table (minus legs) were used. The arena was enclosed by the same testing box as used in the altered sun experiments. The window openings of the plywood box were covered with flat white, plastic-coated cardboard and a 45 cm diameter hole was cut in the center of the top of the box. A single-plane polarizer of 47 x 47 cm, was used to linearly polarize incoming light through the hole. It consisted of a polarizing film sandwitched between 2 sheets of 4 mm plate glass, giving an average 25% light transmittance. The release ring was suspended from a screw-eye siliconed from the center of the polarizer. A small (5x5x5 cm) gray foam block was glued around the screw-eye to dampen vibration and movement of the raised release ring. Crabs were placed into the release ring on the platform through the hole in the top of the box.

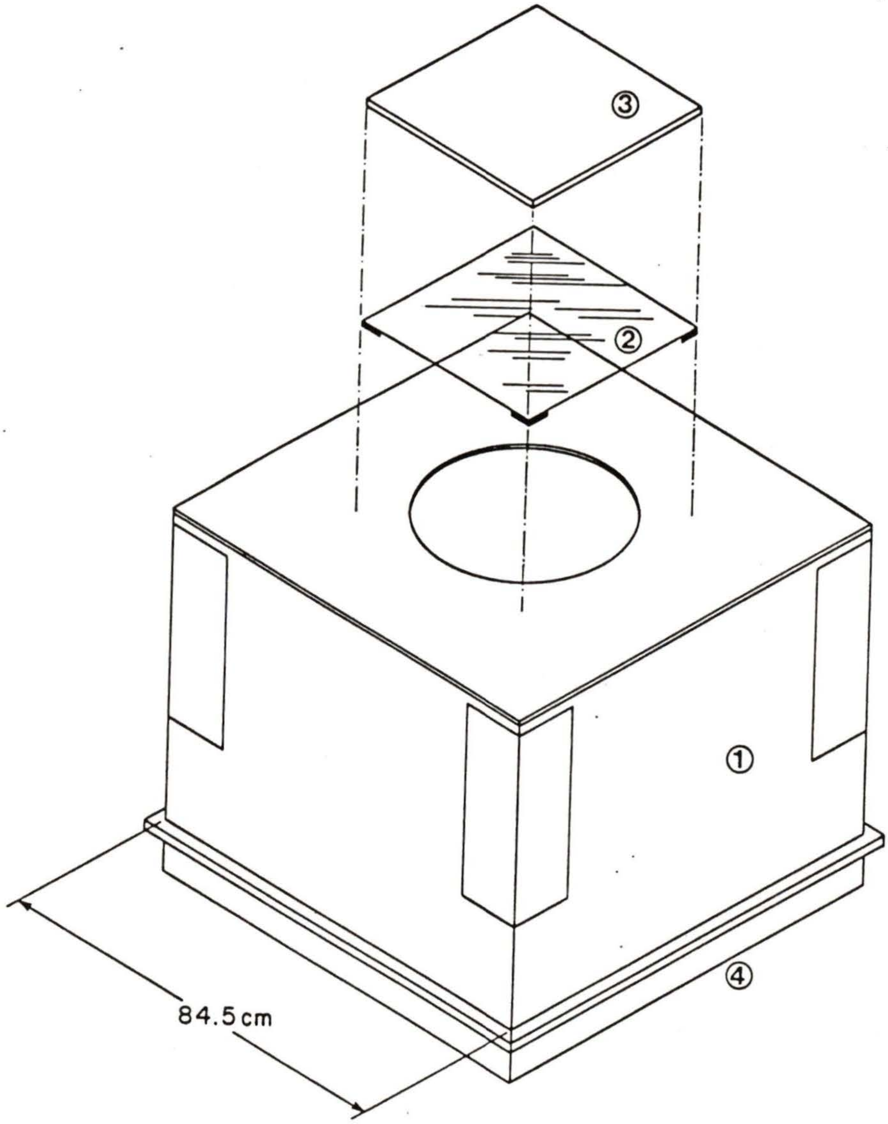
a) OUTDOOR TESTS:

Experimental procedure:

Crabs were collected from the P.B.S. beach (Y-axis = 150°N) and were stored for less than 8 h prior to testing. The outdoor experiments were performed between 1210h - 1750h during Sept.19 - Oct.18, 1984.

The box in all of the outdoor experiments was positioned with one side alligned parallel to 270°N. A control test was performed without the use of the polarizer to determine whether the crabs had enough view of the sky to orient. Further tests were carried out in pairs consisting of a control test and an altered polarization test. The control and altered test pairs were carried out simultaneously by alternating between the control and altered conditions after every 5 crabs tested. The polarizer was removed from the apparatus for the control tests.

Figure 27. Apparatus for testing the polarized light response of the crabs; (1) box aparatus, (2) polarizer, (3) diffuser, (4) support table.


③
②
①
④
84.5 cm

For the initial altered polarization tests, the e-vector of the polarizer was lined up E-W or N-S, and kept in those positions for the duration of the testing period. It was hypothesized that if the crabs responded to the light polarization in a time-compensated manner, then their orientation direction should shift approximately 15°/h counterclockwise, corresponding to the clockwise shift of the sun azimuth. Alternatively, if fixed-angle orientation to the e-vector occured, then the orientation direction would remain constant through time.

In another pair of outdoor tests the e-vector of the polarizer was lined up either parallel or perpendicular to the position of the sun. The polarizer was positioned with respect to the sun after each 10 crabs tested. The average rate of the e-vector axis rotation is about 15°/h clockwise, following the clockwise movement of the sun's azimuth. If the crabs perform time-compensated orientation to the e-vector, then their orientation direction should remain constant through time. The orientation direction was expected to be along the seaward Y-axis of 150°N when the e-vector was perpendicular to the direction of the sun and 90° shifted clockwise and/or counterclockwise when the e-vector was parallel to the sun's bearing. Conversely, if the crabs performed fixed-angle orientation to the e-vector, their orientation direction should be at a constant angle to the e-vector. The 2 different experimental approaches (the fixed and time-compensated e-vector methods) were expected to provide mutually consistent results.

Caution was taken to perform the outdoor experiments in the afternoon so that the sun was not visible to the crabs in the arena. Only reflected sunlight entered the box. Testing was done in an anisotropic light field since a diffuser was not used in these tests.

1. Results of fixed e-vector tests:

Due to the length of time required to test the crabs, some tests could not reach the required 60 crab sample size during one testing session. Thus, results from 2 or more testing sessions were pooled. The experiments which took more than 1 day to reach the required 60 crab sample size have a 4 or 5 digit number code.

The following tests were performed with the polarizer e-vector held fixed in an E-W or N-S position. The results are presented in table 20a.

Test #139 was the first control test to determine whether the crabs were able to orient within the box, but with the polarizer removed. The orientation was highly significant ($p < .001$) (table 20a, fig. 28a), but it was 73° clockwise, and significantly different from the Y-axis direction of 150°N (C.I. test $p < .01$). The box apparatus may have interfered by shifting the directional choice, but since the orientation was highly directed, I decided to continue with tests under altered polarized light.

Both of the other control tests #1404 & #1426, which were performed at the same time as their altered e-vector counterpart tests (table 20a), failed to produce statistically significant orientation ($p > .20$). I conclude that in these tests, the box severely interfered with the orientation of the crabs. It is not known why the initial control test #139 had a highly significant mean bearing while these control tests produced non-significant results since all 3 tests were executed in exactly the same manner.

Both tests with the e-vector W-E (#1415) and N-S (#1437) did not result in statistically significant mean directions ($p > .20$ and $p > .05$, respectively) (table 20a). The mean compass bearing of these two tests were pooled 1) relative to magnetic N and 2) with respect the e-vector axis (and irrespective of the actual compass bearings or position of the sun), by lining up the e-vectors of both tests along a E-W axis.

The data of the 2 pooled tests relative to magnetic N were not

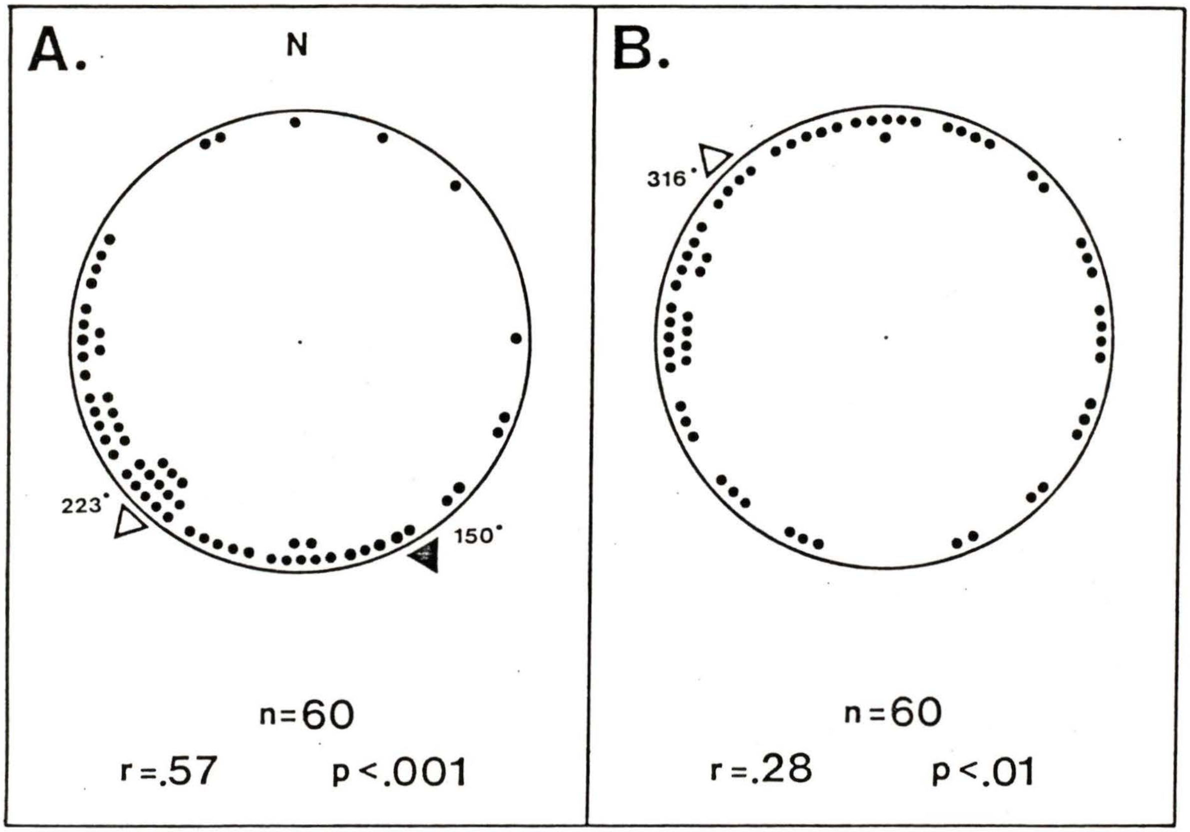
Table 20a: Results of outdoor altered polarization experiments with the P.B.S. beach stock (Y-axis = 150°N) performed under a fixed e-vector. Actual mean compass bearings chosen by crabs relative to N, irrespective of the artificial e-vector axis. Expected direction and mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

test #	e-vector axis	expected direction	n	mean bearing	r-value	p
139	control	150	60	223	.57	< .001
1404	control	150	60	162	.11	> .20
1415	W-E	?	60	51	.11	> .20
1426	control	150	60	87 & 267	.22	> .05
1437	N-S	?	60	230	.21	> .05

Table 20b: Pooled mean compass bearing chosen by crabs in the 2 outdoor altered fixed e-vector tests (#1415 & #1437) pooled relative 1) to magnetic N and 2) with respect to an arbitrarily established E-W e-vector axis. Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

pooled tests relative to	expected direction	n	mean bearing	r-value	p
magnetic N	?	120	228	.05	> .50
W-E e-vector	?	120	347	.12	> .20

Figure 28. Outdoor altered polarization experiments with the P.B.S. beach stock (Y-axis = 150°N) performed under a fixed e-vector. (a) results of initial control test #139. Shown are actual mean compass bearings chosen by crabs relative to N, irrespective of the artificial e-vector axis, (b): converted data of outdoor altered e-vector test #1437 to lie parallel to the sun (see text for explanation).


A.
N
223°
150°
n=60
r=.57
p<.001
B.
316°
n=60
r=.28
p<.01

statistically significant (p> .50) (table 20b), indicating that orientation to any geographically fixed cues did not occur. Since no significant directional preference was revealed by pooling the tests relative to the e-vector (p> .20), I also conclude that significant fixed-angle orientation to the e-vector of the polarizer did not occur.

Since no fixed-angle orientation was evident, a time-compensation conversion was done on the altered e-vector tests (#1415 & #1437) to determine whether the animals performed time-compensated movements to polarized light cues. The data were analyzed with respect to a reallígned polarizer e-vector to the natural e-vector in the sky at that time, either parallel or perpendicular to it. The natural e-vector axis shifts approximately 15°/h in response to the average 15°/h clockwise sun azimuth movement. Assuming that the crabs orient in a time-compensated manner to polarized light cues, the directional trap choice of crabs tested under a fixed artificial e-vector will also shift 15°/h counterclockwise.

Also, since the e-vector of the polarizer was not initially lined up with respect to the position of the sun during testing, an additional adjustment of trap choice had to be made to align the artificial e-vector with respect to the natural e-vector in the sky (and the sun) at the start of testing. The angle in degrees between the azimuth of the sun at the start of testing and direct S was first determined. The value was added to the trap choice of every individual if the sun was past direct S and subtracted if the sun's azimuth was less than 180°N. The results of the converted data are presented in table 20c.

Test #1415 with the e-vector now converted perpendicular to the direction of the sun produced random orientation (p> .20) (table 20c). However, test #1437 with the e-vector converted parallel to the direction of the sun had a significant unimodal mean direction of 316°N (p< .01), not significantly different from the landward Y-axis direction of 330°N (C.I. test p> .05) (fig. 28b). This result

Table 20c: Converted data of outdoor altered e-vector tests #1415 and #1437 with respect to a time-compensated e-vector (see text for explanation). Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

test #	fixed e-vector converted to	expected direction	n	mean bearing	r-value	p
1415	perpend. to sun	?	60	3 & 183	.15	> .20
1437	parallel to sun	?	60	316	.28	< .01

Table 21a: Time-compensated outdoor tests. Actual mean compass bearings chosen by crabs with respect to N and the direction of the sun. Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

test #	e-vector axis relative to sun	expected direction	n	mean bearing	r-value	p
16671	perpendicular	150	60	176	.12	> .20
16771	parallel	?	60	149	.17	> .10

suggests that the crabs oriented in a landward Y-axis direction in a time-compensated manner with respect to the position of the W-E e-vector. The reason for the inconsistent results in these 2 tests is not known.

2. Results of time-compensated tests;

Time-compensated outdoor altered e-vector tests were next performed to try to confirm the apparent time-compensated orientation ability to the e-vector seen in one of the prior fixed e-vector tests which was corrected for time-compensation (#1437).

Two tests were performed in which the polarizer e-vector was realligned with respect to the changing position of the sun (and thus the natural e-vector in the sky) during testing. The perpendicular test (#16671) had the e-vector of the polarizer lined up with that of the ambient sky. The latter is also primarily in a plane perpendicular to the direction of the sun. Thus the expected orientation direction was the seaward Y-axis direction (150°N). The parallel test (#16771) had the e-vector of polarization perpendicular to that of the normal sky. It was difficult to predict how the crabs would respond to this type of shift. The results of the 2 tests are presented in table 21a.

Both time-compensated tests #16671 and #16771 had non-significant mean bearings ($p > .20$ and $p > .10$, respectively) (table 21a), suggesting that no time-compensated orientation with respect to the e-vector of polarization occured. These results contradict the significant results obtained in test #1437 converted to time-compensated data in which evidence of time-compensated orientation was obtained (section a).

The results of the 2 tests were pooled with respect to magnetic N and with respect to an arbitrarily established e-vector parallel to the direction of the sun (in the manner previously described) in order to increase the sample size and detect weak orientation trends. The results are given in table 21b.

Table 21b: Pooled mean compass bearings chosen by crabs in outdoor tests #16671 & #16771) 1) pooled relative to N, and 2) by lining up the results of both tests with respect to an arbitrarily established e-vector parallel to the direction of the sun. Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

pooled tests relative to	expected bearing N	sample size	mean bearing	r-value	p
magnetic N	?	120	161	.14	> .05
e-vector	?	120	193	.08	> .50

Table 21c: Conversion of outdoor tests #16671 & #16771 to non-time-compensated bearings. Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

test #	e-vector converted to	expected direction	n	mean bearing	r-value	p
16671	W-E	?	60	177 & 357	.12	> .20
16771	N-S	?	60	175 & 355	.14	> .20

The pooled data relative to N and relative to an arbitrarily established e-vector parallel to the direction of the sun did not produce a significant orientation direction (p> .05 and p> .20, respectively) (table 21b). Again, these results indicate that the crabs tested outdoors did not show significant orientation with respect to the e-vector of polarization in a time-compensated manner. Interestingly, the pooled data relative to magnetic N had a non-significant mean bearing (161°N), close to the seaward Y-axis direction of 150°N.

To confirm that the crabs did not perform fixed-angle orientation to the e-vector, as was postulated in section a above, the data of these time-compensated tests #16671 and #16771 were transformed into non-time-compensated bearings. The position of the polarizer e-vector for each test crab was taken and rotated (along with the crab's bearing) so that the e-vector was alligned either N-S in the case of the parallel test, or E-W for the perpendicular test. This was done by the exact reversal of the procedure used for converting fixed e-vector data to time-compensated data. The results are given in table 21c.

Results of both conversions to non-time-compensated data showed similar bimodal mean bearings to the N and S, but both results were non-significant (p> .20) (table 21c). These results indicate that the crabs did not show fixed-angle orientation to the artificial e-vector, and are in agreement with the results obtained in section a above.

b) INDOOR TESTS:

Indoor experiments were performed to eliminate possible outdoor sources of interference such as differential light intensity within the box, due to the sun's position.

Experimental procedure:

Crabs were collected from the P.B.S. beach (Y-axis = 150°N), and were stored for no longer than 8 h prior to testing. The indoor tests were all done between 1230h - 1650h between Oct.26 - Oct.31, 1984 in the same lightproof laboratory room at the Pacific Biological Station as the artificial sun tests.

An artificial light source was centered 97 cm above the box to minimize directional shadows within the box and provide an isotropic light field above it. The light source was the same artificial sun used in previous tests, a 500 W color-corrected incandescent bulb. A diffuser of the same size as the polarizer, made of 4 mm thick translucent white lucite, was used between the artificial light source and the polarizer. The e-vector was either positioned W-E, or N-S and left in those positions for the duration of each test.

One side of the box was always aligned parallel to 290°N to observe any effect of the box position. Two pairs of tests were performed, with each test in the pair having the polarizer e-vector set perpendicular to the one in the other test. Each set of 2 tests were performed simultaneously during the same testing session by changing the direction of the polarizer after every 5 crabs tested. No control experiments were performed with the polarizer removed, since orientation indoors was not expected without polarized light cues as this was the only visual directional cue provided to the crabs. However, each test effectively acted as a control for the other in the pair.

If the crabs used polarized light cues in their orientation, they could either 1) show a time-compensated shift in their orientation direction or 2) fixed-angle orientation with respect to the position of the e-vector of the polarizer.

Results:

Due to the length of time required to test the crabs, some tests could not reach the required 60 crab sample size during one testing session, and thus results from 2 or more testing sessions were pooled. The experiments which took more than 1 day to reach the required 60 crab sample size are denoted by a 4 or 5 digit number. The results for the 4 indoor tests conducted under a fixed polarizer e-vector are presented in table 22a.

The 4 tests all failed to show significant orientation (p> .10 to p> .50) (table 22a), indicating that fixed-angle orientation to the e-vector did not occur.

The 4 tests pooled relative to magnetic N and relative to an arbitrarily established E-W e-vector, also produced non-significant results (p> .20 and p> .50, respectively) (table 22b), confirming that the crabs did not perform fixed-angle orientation to the e-vector of polarization.

The pooled data were then converted to time-compensated bearings, to determine if time-compensated orientation to the e-vector occured indoors, and then pooled relative to N and relative to the e-vector. The results were again not significant (p> .50 and p> .20, respectively) (table 22c). I thus conclude that the crabs tested indoors failed to orient to the e-vector of polarized light in a time-compensated manner.

The non-significance of the outdoor and indoor results prompted one additional statistical analysis, since non-symmetric, multimodal fixed-angle orientation to the e-vector has been found in various species of invertebrates, including decapods. For example, juvenile ghost crabs, Ocypode ceratopthalma, orient perpendicular, parallel, and at 45° diagonal to the e-vector (Daumer et al., 1963). This type of orientation may not have been detected by the normal statistical analyses used. Thus the outdoor and indoor tests in which the polarizer

Table 22a: Results of indoor altered polarization experiments with the P.B.S. beach stock (Y-axis = 150°N). Mean compass bearings chosen by crabs irrespective of the polarization axis and time of day (not time-compensated). Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

test #	polarizer e-vector	expected direction	n	mean bearing	r-value	p
172	W-E	?	60	16	.19	> .10
173	N-S	?	60	305	.09	> .50
1756	W-E	?	60	150	.07	> .50
1747	N-S	?	60	100	.15	> .20

Table 22b: Pooled mean compass bearings chosen by crabs in indoor tests #172, #173, #1756 and #1747 1) pooled relative to N, and 2) by lining up the results of all tests with respect to an arbitrarily established W-E e-vector. Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

all tests pooled relative to	expected direction	n	mean bearing	r-value	p
magnetic N	?	240	46	.05	> .20
W-E e-vector	?	240	66	.03	> .50

Table 22c: Pooled indoor tests converted to time-compensated bearings. Mean bearings are in °N, n = sample size, p = probability, and ? = expected direction could not be established.

fixed e-vector converted to	expected direction	n	mean bearing	r-value	p
parallel to sun	?	120	98	.07	> .50
perpendicular to sun	?	120	187	.10	> .20

e-vector was held constant E-W or N-S were analyzed for this type of multimodal orientation. The orientation angle preferences to the e-vector of each test crab were analyzed for inequality of frequency in the 16 possible trap directions by the Chi-squared test, which would unveil multiple bimodal orientation directions which were not necessarily symetrically opposed, such as in quadrimodal orientation. It would also unveil multiple, unimodal orientation directions which were not symetrically opposed.

Five possible orientation axes were analyzed in the above manner, namely parallel, perpendicular, and at angles of 22.5°, 45°, and 67.5° to the e-vector axis. The frequencies of trap choices in these directions in the pooled tests were not significantly different from uniformity (Chi-squared test $p > .30$). The results of this analysis indicate that the crabs did not perform any type of oriented movements with respect to the e-vector, but instead oriented randomly.

CONCLUDING REMARKS

The crabs showed significant orientation in the first outdoor control experiment suggesting that sufficient sky cues were available through the hole in the box. However, the mean direction observed in this control test was different from the seaward Y-axis. The other 2 control tests produced random results. This suggests that physical factors of the box interfered with direction finding. The abrupt shift in light intensity when the animals were introduced into the box, coupled with the physical nature of the box, may have been responsible for the lack of proper orientation in all tests.

Persistent lack of orientation resulted once the polarizer was introduced. The pooled results of the outdoor N-S fixed e-vector tests, however, did become statistically significant after they were converted to time-compensated bearings (table 22c), suggesting that in this case the crabs were oriented in a time-compensated manner with respect to the

N-S e-vector axis. However, in view of all of the other non-significant results, the validity of this result must be questioned and any conclusions must remain purely speculative.

Brines (1980) pointed out that the natural polarization pattern in the blue sky is quite complex. The skylight polarization pattern rotates about the anti-sun pole point in the north sky with respect to the sun's position. The azimuth of the pole point is an important orientation cue, as it provides true compass direction, in the same way as Polaris does. It is thus possible that if the crabs use polarized light cues, they may require such information for correct orientation, information which was not provided to them by the testing apparatus. Another confusing factor may have been reflection in the apparatus, since it is known that in test arenas using linearly polarized light, walls perpendicular to the e-vector have a greater light reflection (Jander and Waterman, 1960).

I thus conclude that either 1) the crabs do not use polarized light cues in orientation or 2) the crabs are capable of using the cues, but the experimental apparatus interfered with the response.

4. PLANETARIUM EXPERIMENTS

INTRODUCTION

The purpose of these experiments was to determine if H. nudus were capable of using stellar orientation cues. The tests were performed in the H.R. Macmillan Planetarium in Vancouver, B.C. In the planetarium, star patterns (not including planets) could be rotated horizontally so that stellar N and the rest of the stellar coordinates would lie in different compass directions than normally found in nature. It was postulated that if the crabs use stellar cues in orientation, their directional preferences should shift correspondingly to the shifts in the star pattern. This method has been successfully used by researchers working on bird orientation (Sauer, 1957, 1961; Sauer and Sauer, 1960; Kramer, 1952, 1957; Emlem 1966, 1970).

EXPERIMENTAL PROCEDURE

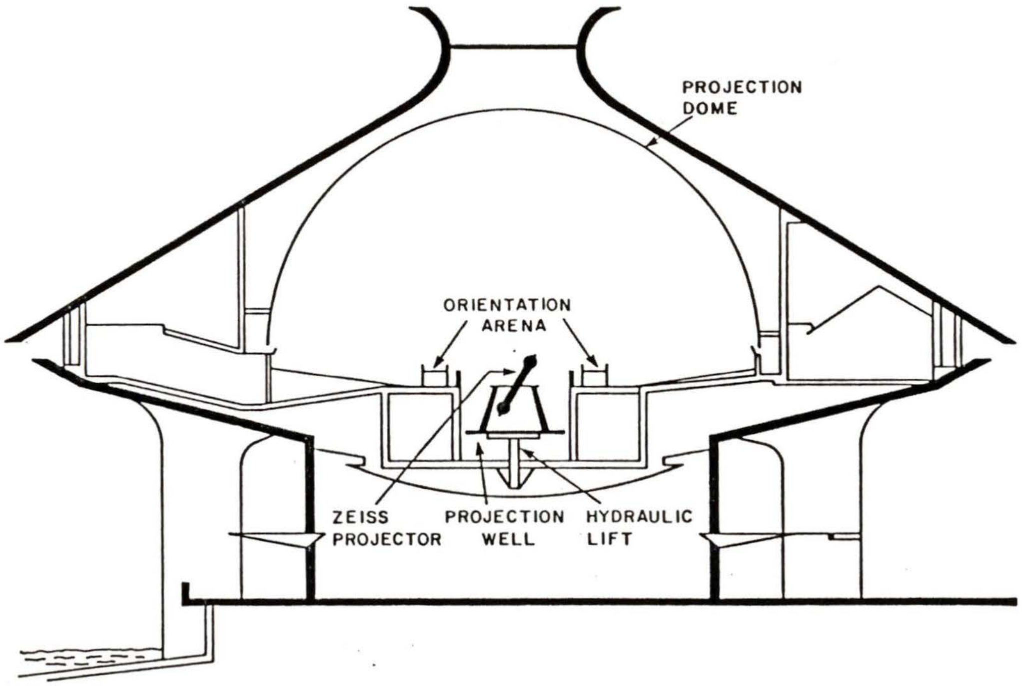
Specimens were collected from 29th. Street beach (X-axis = 125°N & 305°N) in West Vancouver and were transported by car from their collection areas to the holding facility at the Fisheries and Oceans West Vancouver Laboratory in plastic collection buckets with lids. There, they were stored in 250 gallon oval light blue fiberglass tanks with running sea water for less than 40 h prior to testing.

A Zeiss star projector projected the star pattern in the planetarium (fig. 29a). This machine produced a correct star pattern for the locality and testing date. However, the sky lower than about 20° above the horizon was not projected due to the restrictive size of the planetarium dome. The star pattern could be rotated horizontally and vertically so that stellar N could be positioned in any chosen position on the dome. Absolute and relative star light intensity were held close to ambient. Since it was impossible to revolve the planetarium sky with the speed of natural rotation, the star patterns were held stationary for the duration of each experiment.

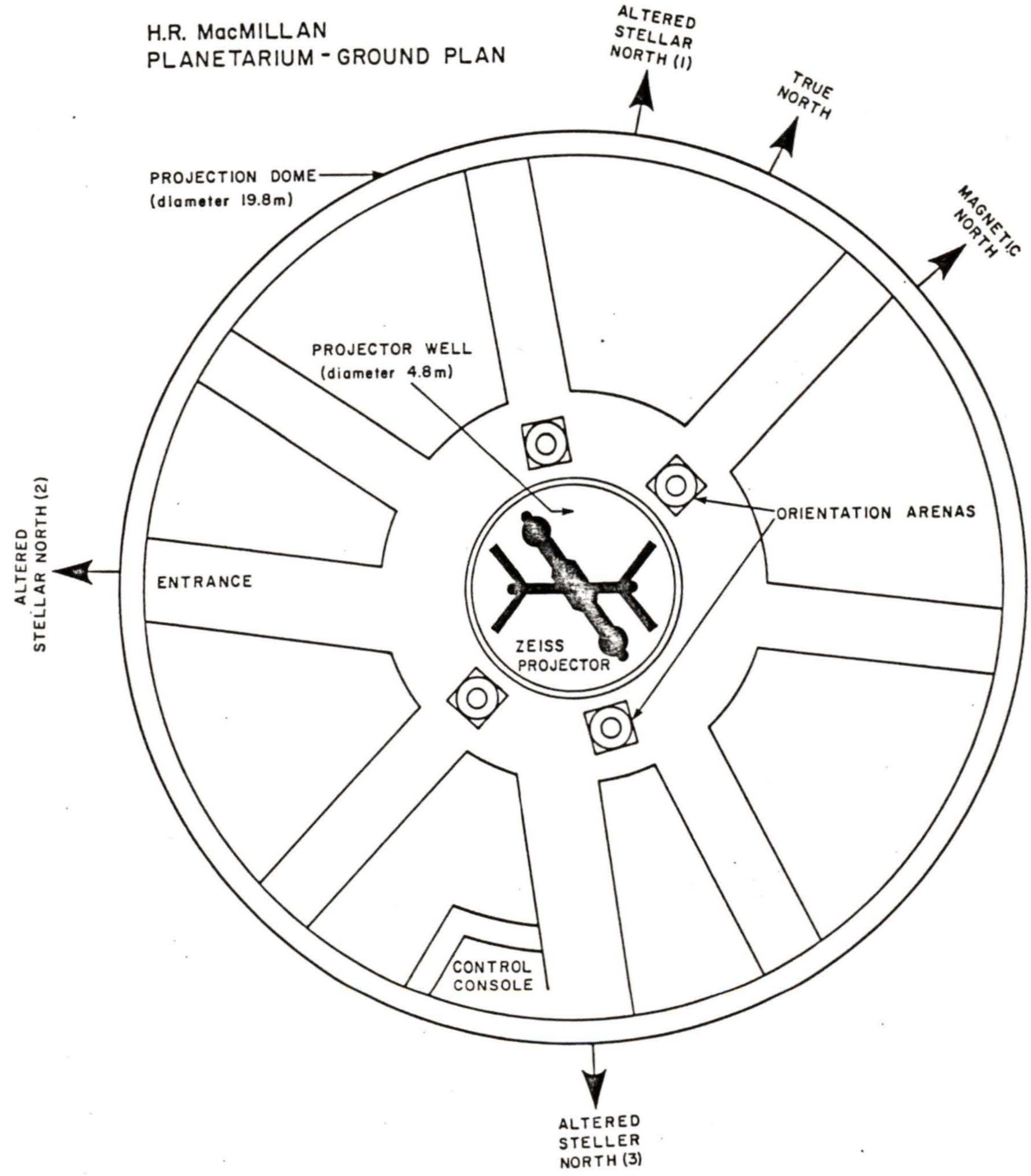
Figure 29. Experimental layout of altered star experiments; (a): Cross-section view of the H.R. MacMillan planetarium in Vancouver, B.C., (b): top view of the experimental layout in the planetarium.

A.

H.R. MacMILLAN PLANETARIUM - CROSS SECTION



B.


H.R. MacMILLAN
PLANETARIUM - GROUND PLAN
ALTERED STELLAR NORTH (1)
TRUE NORTH
MAGNETIC NORTH
PROJECTION DOME
(diameter 19.8m)
PROJECTOR WELL
(diameter 4.8m)
ORIENTATION ARENAS
ALTERED STELLAR NORTH (2)
ENTRANCE
ZEISS PROJECTOR
CONTROL CONSOLE
ALTERED STELLER NORTH (3)

Three different positions for stellar N were selected so as to obtain the largest possible arc between successive positions and also to stay within the rotation limits of the star projector (fig. 29b). The projector performs more optimally at certain positions by providing a clearer, less distorted view of the sky at the outermost edges of the dome. Also, the projector could not be rotated so as to match the projector stellar N exactly with the real stellar N for control purposes, due to blockage of the path by a number of small projectors. Unless otherwise stated, all directions in this paper refer to magnetic compass directions where magnetic N is 0° (or 360°). The term "true N" is a synonym for "stellar N". Magnetic N measured in Vancouver lies at 24° east of true N.

Control experiments with a starless, diffusely illuminated planetarium dome could not be performed due to concurrent use of the planetarium by other researchers. However, the 3 positions selected for the shifted stellar N would effectively act as each others' controls.

The position of the first manipulated stellar N was at 318°N. This position was 18° to the west of the real stellar N. Thus crabs responding to the shift should correspondingly change their orientation 18° to the west. The next position for stellar N was at 220°N, which was a 116° shift to the west from magnetic N. The third position for stellar N was at 126°N, which was equivalent to a 150° shift to the east of magnetic N.

The crabs were transported by car from the holding tanks at the West Vancouver Laboratory to the planetarium, in white plastic buckets with lids filled with sea water. In total, 6 experiments were conducted from Feb. 16-24, 1984.

Orientation arena #2 and the support table were used. The arena was randomly positioned excentric of the star projector. The hole in the table was uncovered and test crabs were visually observed by the experimenter laying motionless underneath the table and viewing the animals on the clear plexiglass platform. All testing took place between 0630h and 0930h. All planetarium lights except for the star projector were turned off 5 min prior to each experiment and kept off for the duration of the testing session. At the same time, bucket lids were removed and the crabs were given a 5 min period to adjust to their surroundings. The only other light source that the crabs were exposed to were small 3 V flashlights with red filters used for retrieving crabs from the traps and to record data. Crabs were given 1 min in the ring and 1 min to make a trap choice after release.

RESULTS

Due to the available time in the planetarium, it was not always possible to reach the optimum sample size of 60 crabs. Three tests had statistically significant results (table 23, fig. 30). Test #90 had bimodal mean bearings of 136°N & 316N. These were not significantly different from the X-axis directions of 125°N & 305°N (Bearing deviation test p> .25), but were different from the bimodal directions of 9°N & 189°N based on the shifted stellar coordinates (fig. 30a). Tests #92 and #96 had unimodal mean bearings of 140°N and 322°N, respectively. These directions are similar to one of the X-axis directions of 125°N & 305°N (C.I. tests p> .05), but not to the nearest directions of 95°N and 9°N (respectively) based on the shifted stellar coordinates (fig. 30b,e).

Tests #93 and #95 showed non-significant bimodal mean bearings, but were within at least 48° of the X-axis directions of the crabs' home beach (125°N & 305°N) (fig. 30b-e). These results indicate that the crabs were maintaining their X-axis directions in the planetarium, irrespective of the star configurations.

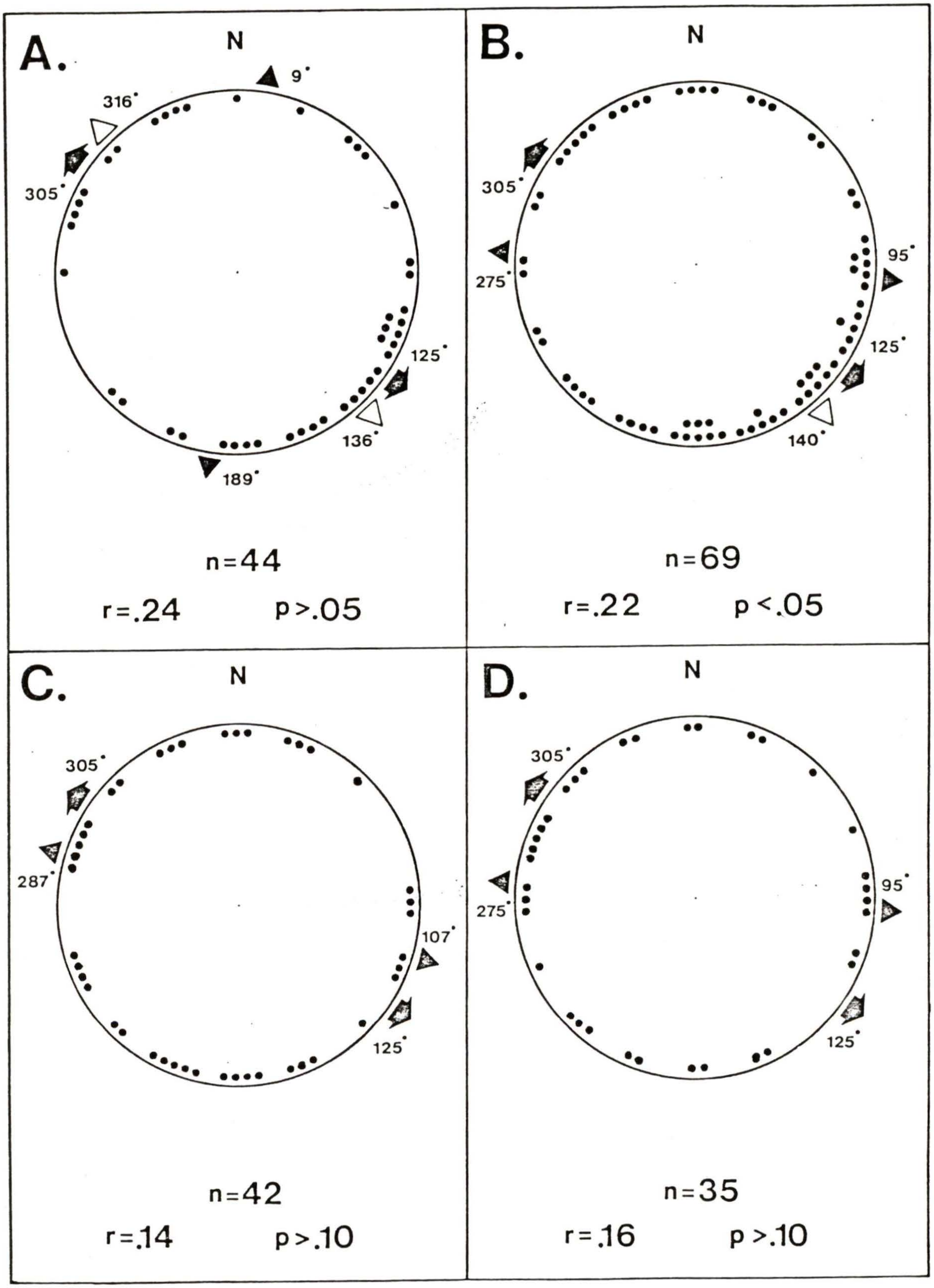
The directions taken by the total of 231 crabs tested were pooled relative to the actual magnetic N, and then pooled relative to the

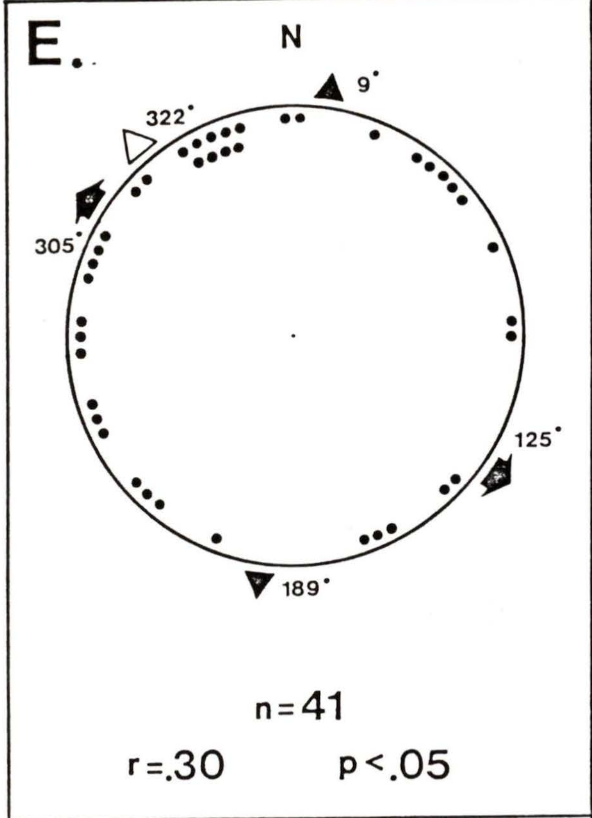
Table 23: Directional data for planetarium experiments with shifted stellar coordinates for the 29th Street beach stock (X-axis = 125°N & 305°N). X-axis, mean bearings, and stellar N are in °N, n= sample size, and p = probability.

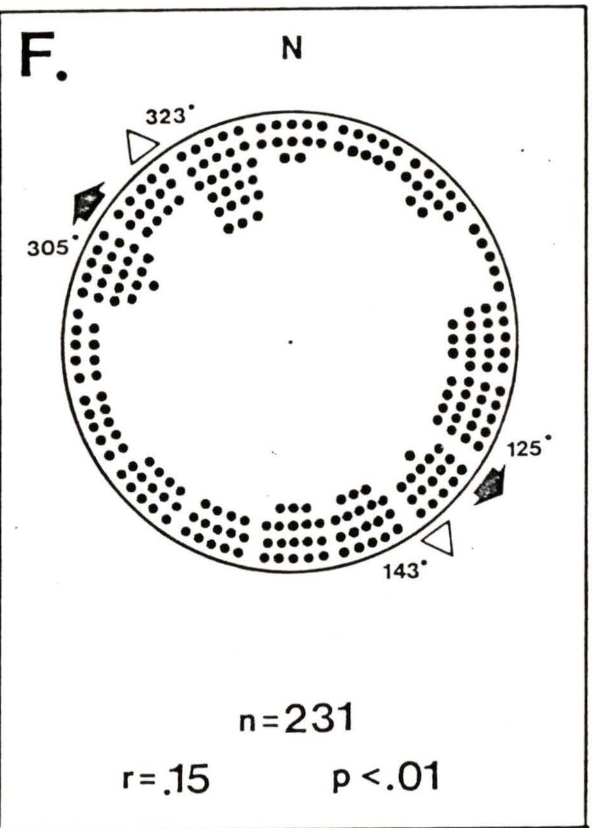
test #	real X-axis	shifted N		shifted X-axis	n
		stellar	magnetic		
90	125 & 305	220	244	9 & 189	44
92	"	126	150	95 & 275	69
93	"	318	342	107 & 287	42
95	"	126	150	95 & 275	35
96	"	220	244	9 & 189	41

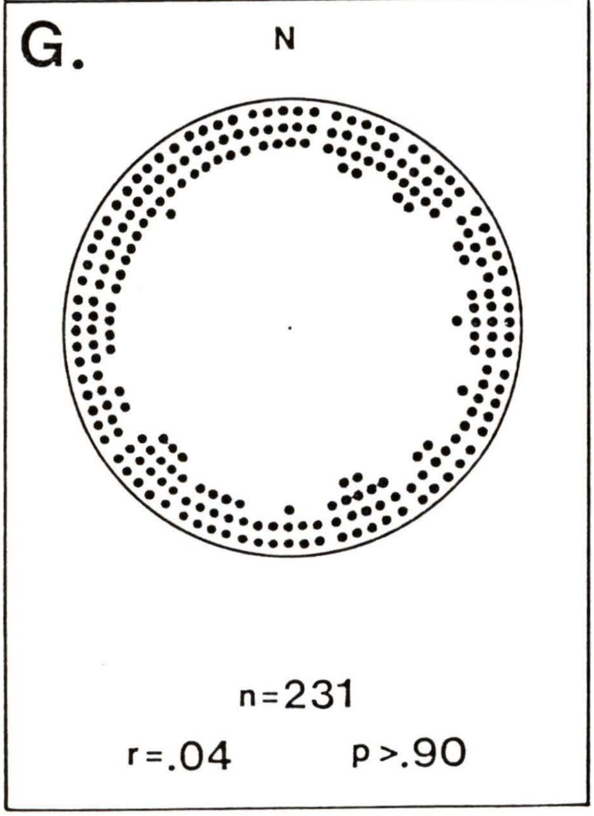
test #	bimodal mean bearings	r-value	p	unimodal mean bearing	r-value	p
90	136 & 316	.30	< .02	128	.24	> .05
92	149 & 329	.20	> .05	140	.22	< .05
93	173 & 353	.13	> .20	233	.14	> .10
95	107 & 287	.13	> .50	289	.16	> .10
96	146 & 326	.08	> .50	322	.30	< .05

Figure 30. Directional data for planetarium experiments with shifted stellar coordinates for the 29th Street beach stock (X-axis = 125°N & 305°N); (a-e): individual tests #90, #92, #93, #95, and #96 (respectively), (f): pooled analysis of the 4 tests relative to normal magnetic N, and (g): relative to the shifted stellar N. Arrows indicate actual X-axis, solid triangles represent shifted X-axis based on the shifted stellar coordinates, open triangles signify mean bearings.


A.
N
9°
316°
305°
125°
136°
189°
n=44
r=.24 p>.05
B.
N
305°
275°
95°
125°
140°
n=69
r=.22 p<.05
C.
N
305°
287°
107°
125°
n=42
r=.14 p>.10
D.
N
305°
275°
95°
125°
n=35
r=.16 p>.10


E.
N
9°
322°
305°
125°
189°
n=41
r=.30
p<.05


F.
N
323°
305°
125°
143°
n=231
r=.15
p<.01


G.
N
n=231
r=.04
p>.90

shifted stellar N, the latter by lining up all of the manipulated stellar norths to coincide at the 336°N magnetic compass direction of the outside stellar N. This analysis would unequivocally determine what type of orientation the crabs were performing. The results are presented in table 24.

Pooling the data of all 231 crabs relative to magnetic N gives a statisically significant bimodal mean bearing of 143°N & 323°N ($p< .01$) (table 24). This is within 18° of the X-axis directions of 125°N & 305°N (fig. 30f). When all of the 29th Street tests were pooled relative to the stellar coordinates, the result was not significantly different from uniformity ($p> .90$), indicating that the crabs did not respond to the stellar rotation (fig. 30g). From these results I conclude that the crabs did not respond to the stellar orientation cues, but oriented along the X-axis directions of their home beach when tested within the planetarium.

CONCLUDING REMARKS

The crabs did not respond to the shifted star pattern and thus no conclusions can be made as to their ability to use stellar cues in orientation. Perhaps H. nudus are not able to orient by stellar cues, or do so only during certain times or seasons. Another possibility is that the crabs are capable of using stellar cues, but they ignored the artificial projection due to its shifted positions, because of parallax problems, which occur in planetarium projections.

The ability of H. nudus to orient with respect to their home beach in the planetarium is remarkable. The bimodal X-axis orientation observed is similar to that observed in the outdoor tests performed with the same population (Chapter IV) and also to van Tets' (1956) results with different populations from the Vancouver area. The animals must have used non-visual cues, similar as during the completely overcast outdoor night tests with the Nanaimo crabs (Chapter V). The most obvious possibility is orientation by the use of magnetic cues. Even though the

Table 24: Pooled analysis of the 29th Street stock (X-axis = 125°N & 305°N) 1) relative to normal magnetic N and 2) relative to the shifted stellar N. X-axis and mean bearings are in °N, n= sample size, and p = probability.

pooled relative to	n	X-axis	mean bearing	r-value	p
normal magnetic N	231	125 & 305	143 & 323	.15	< .01
shifted stellar N	231	125 & 305	336	.04	> .90

dome structure of the planetarium contains large amounts of metal, magnetic anomalies in the dome could not be detected by the use of a hand-held compass.

A pooled sample of 231 crabs was required to detect orientation in the planetarium since individual tests provided small r-values. This pooled sample was about 2 times the size required to detect significant orientation trends with the same population in the outdoor tests (Chapter IV), where a sample size of 114 crabs was used to detect orientation trends. This suggests that non-visual cues may give less directional information than visual ones.

b) Non-visual orientation cues.

5. ALTERED MAGNETIC FIELD TESTS

INTRODUCTION

The purpose of these experiments was to examine the possible use of magnetic cues by H. nudus in Y-axis orientation. It was suspected that H. nudus could use geomagnetic cues for orientation due to the ability of the crabs to orient in the planetarium experiments (Chapter VIIa) and in the overcast night trials and daytime covered tests (Chapter VI).

Some species of animals are known to be able to orient by the use of geomagnetic cues. Examples are sparrows (Bingman, 1981), salamanders (Phillips, 1977; Phillips and Adler, 1978), sockeye salmon, Onchorhynchus nerka (Quinn, 1980; Quinn and Brannon, 1982; Quinn et al., 1981), bees (Lindauer and Martin, 1972), flour beetles, Tenebrio molitor (Arendse, 1978), amphipods (Arendse, 1978; Arendse and Barendregt, 1981; Arendse and Kruysujk, 1981), snails (Barnwell and Brown Jr., 1962, Brown et al., 1960), and bacteria (Blakemore, 1975).

The earth's magnetic field consists of 3 major components; the x-component (horizontal component), vertical component (inclination), and the field intensity. The x-component of the magnetic field provides geographical directionality.

For the magnetic field experiments, a Rubens coil was used to alter the x-component of the magnetic field (Rubens, 1945). I reasoned that if the crabs were able to utilize magnetic cues in their orientation, their directional preference should shift with respect to the shifts in the magnetic field.

APPARATUS

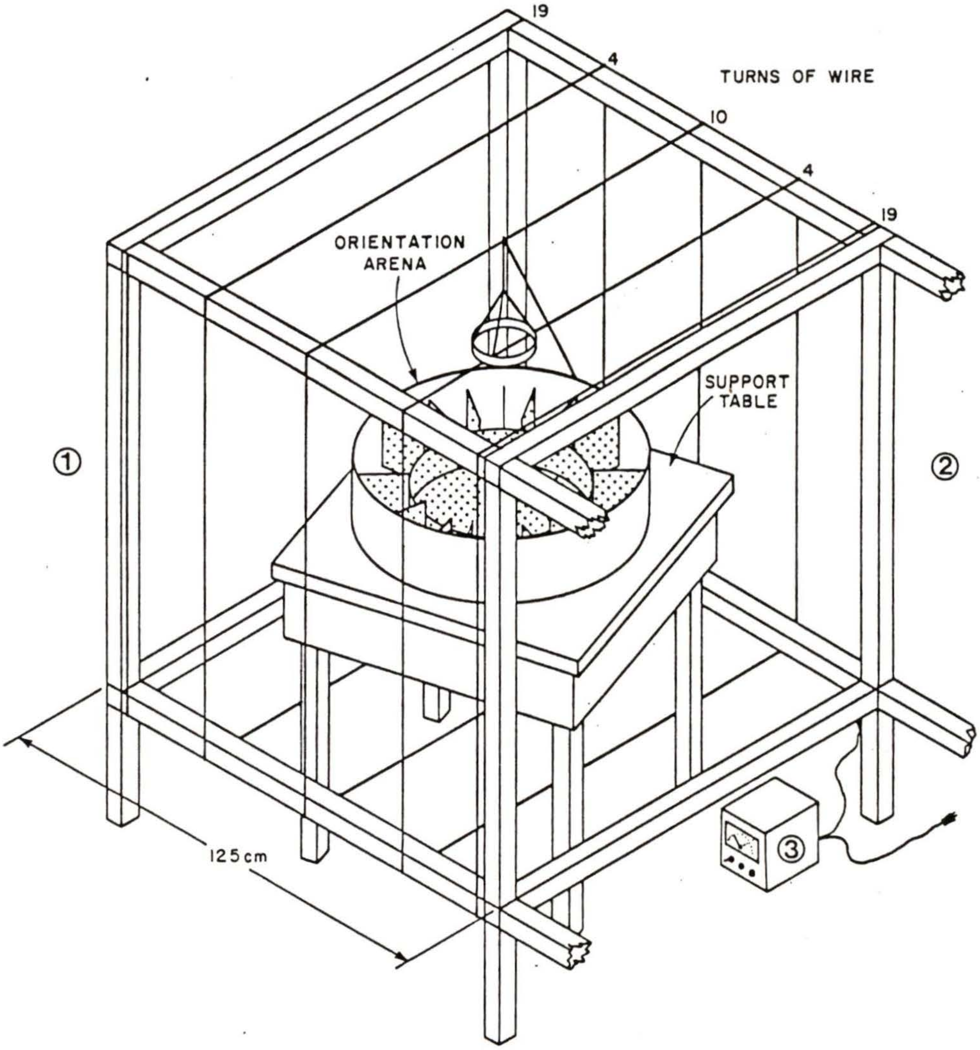
The experimental apparatus is shown in fig. 31. The Rubens coil was used to rotate the horizontal component (x-component) of the magnetic field in the arena (Rubens, 1945). The coil creates a magnetic field perpendicular to the copper wire windings, which combined with the ambient field of the earth produced a resultant x-component by vector addition. The resultant x-component could be rotated 90° clockwise, and 90° counterclockwise by rotating the coil counterclockwise and clockwise. The coil was powered by a 5 A DC transformer.

The Rubens coil provides a uniform magnetic field over a considerable volume (Rubens, 1945). The coil does not substantially affect the magnetic field intensity or inclination (Quinn, 1980). Deviation of the x-component of the magnetic field from its value at the center of the coil is only 1% at half the coil diameter and 5% at a distance of 90% of the coil diameter (Rubens, 1945). The large volume allowed orientation arena #2 and support table to be used inside it (fig. 31), while ease of access made it possible to efficiently test the crabs.

The size of the Rubens coil was 125x125x125 cm and it was mounted on 30 cm long legs. An addition of the same dimensions was attatched to one side of the coil and housed the experimenter, crab buckets, and recording apparatus. The whole apparatus was constructed with non-magnetic metals and materials.

The center of the arena platform was positioned in the volumetric center of the coil. This was done to ensure that a uniform magnetic field was present on the platform. Distortion of the magnetic field could only be detected within 10 cm of the coil edges with a handheld compass. This distance was well outside the reach of the testing platform whose edge was at least 37 cm from the sides of the coil. No magnetic anomalies could be detected within the orientation arena with a magnetic compass,

Figure 31. Experimental apparatus for altering the horizontal component of the geomagnetic field; (1) observer housing, (2) Rubens coil, (3) power supply. The cover and the whole observers section are not shown for clarity.


19
4
TURNS OF WIRE
10
4
19
ORIENTATION ARENA
SUPPORT TABLE
①
②
③
125 cm

with the coil turned on or off. The orientation arena was only 63% of the horizontal coil width. Based on Rubens' (1945) calculation, the deviation of the magnetic field x-component from its value at the center of the platform was less than 5% at the edge of the orientation arena. The system was continually monitored during testing with a handheld compass positioned below the support table. Two handheld Silva Ranger 15TDCL compasses (Silva Ltd., Willowdale, Ont.) were standardized against each other and used in all of these experiments. The release ring on the platform was suspended from one of the crossbars on the top of the coil, and the wooden dowel ring supports were not used (fig. 31). Both the orientation arena platform and the coil were levelled with a carpenter's level.

The whole apparatus, including the experimenter portion, was completely covered to restrict visual orientation cues. The roof and upper 40 cm of the cage was covered in a waterproof, opaque white plastic-coated canvas. This cover extended down to the base of the support table within the coil, and prevented any direct outside light from entering the orientation arena. The ends of the canvas were extended to the ground by translucent white cotton sheeting, to complete the cover. The cotton provided evenly diffused non-directional illumination into the cage, which was necessary in order to conduct the tests in sufficient daylight. An added feature of the cloth was that it depolarized the incoming light source. Testing under all weather conditions was possible because of the waterproof roof. Even though the cotton siding ocassionally got wet, rain did not penetrate through and the quality of visible light entering the apparatus did not noticeably change.

EXPERIMENTAL PROCEDURE

Thirteen experiments were conducted between Sept. 1-17, 1984. Crabs were collected from the P.B.S. beach (Y-axis = 150°N) and transported to the holding and testing facility on foot in open buckets. They were stored for less than 3 h prior to testing.

The experiments were performed between 1130h - 1800h under sky conditions ranging from 0% to 100% overcast and rain. Prior to each test, crabs were placed into the experimenter's area of the cage. They were kept in the opaque white plastic collecting buckets with lids at all times to ensure that the crabs were not affected by the visual presence of the adjacent observer. The observer was not visible to the test animals on the platform.

The control experiments were performed in an unaltered magnetic field with the power to the coil shut off. Four altered field tests had magnetic N displaced to the E (90° clockwise) and 3 to the W (90° counterclockwise) from its normal position.

In order to determine possible effects of the coil and/or cover on orientation, one test was performed within the cage but with the entire cover removed in an unaltered field under a 45% overcast sky. The results from this test were to be compared to the other control tests performed under cover, and also to other tests conducted with the same population. In this way, any effects of the apparatus on the orientation would be detected. If any discrepancy in the orientation direction was found between this test and the other magnetic control tests conducted under cover, an effect of the cover would be revealed. If this test differed significantly from other tests, an effect of the physical structure of the coil would be revealed.

RESULTS

The results are presented in tables 25 and 26, and figs. 19, 33, and 34. The 4 control tests (table 25a) showed an approximate 180° shift to 326°N in their directional preference, from the 150°N seaward Y-axis direction (fig. 19f). As explained in Chapter VI, the crabs sometimes shift their orientation direction to the landward Y-axis direction of 330°N when the sky becomes completely overcast or obstructed. The expected direction for the control tests was thus taken to be 330°N

Table 25a: Directional results of control magnetic field tests with the P.B.S. beach crabs (Y-axis = 150°N). n = sample size, Y-axis and mean bearings are in °N, and p = probability.

test #	test condition	n	Y-axis	mean bearing	r-value	p
126	countercl. controls	60	150	347	.38	< .001
128	" "	60	150	283	.30	< .005
countercl. controls pooled		120	150	319	.29	< .001
130	clock. controls	60	150	325	.19	> .10
132	" "	60	150	142 & 322	.12	> .20
clock. controls pooled		120	150	344	.12	> .10
all controls pooled		240	150	326	.20	< .001

(table 25a), and the results from the altered field tests were compared against this direction, rather than against the seaward Y-axis direction of 150°N.

To determine any effect of the allignment of the testing apparatus in the clockwise and counterclockwise testing positions, the results from the clockwise and counterclockwise controls were compared (table 25a). The mean bearings were 319°N for the pooled counterclockwise controls and 344°N for the pooled clockwise tests. It is unlikely that the 90° testing position rotation was responsible for the difference of 25° in the mean bearing between the two test conditions. I thus conclude that a significant effect of the Rubens coil or experimenter cage on the directional preference was not present.

In the altered magnetic field experiments, not all tests in the same testing condition could be established to have statistically indifferent mean directions. However, the data were still pooled to show the average direction preferences more clearly. When the 4 clockwise shifted tests (#131, #133-#135, table 25b, fig. 32a-d) were pooled, a statistically significant unimodal mean bearing of 29°N ($p < .05$) was obtained (fig. 32e). This mean bearing was not significantly different from the expected 90° clockwise shifted direction of 60°N (C.I. test $p > .05$), but was different from the landward Y-axis direction of 330°N (C.I. test $p < .05$).

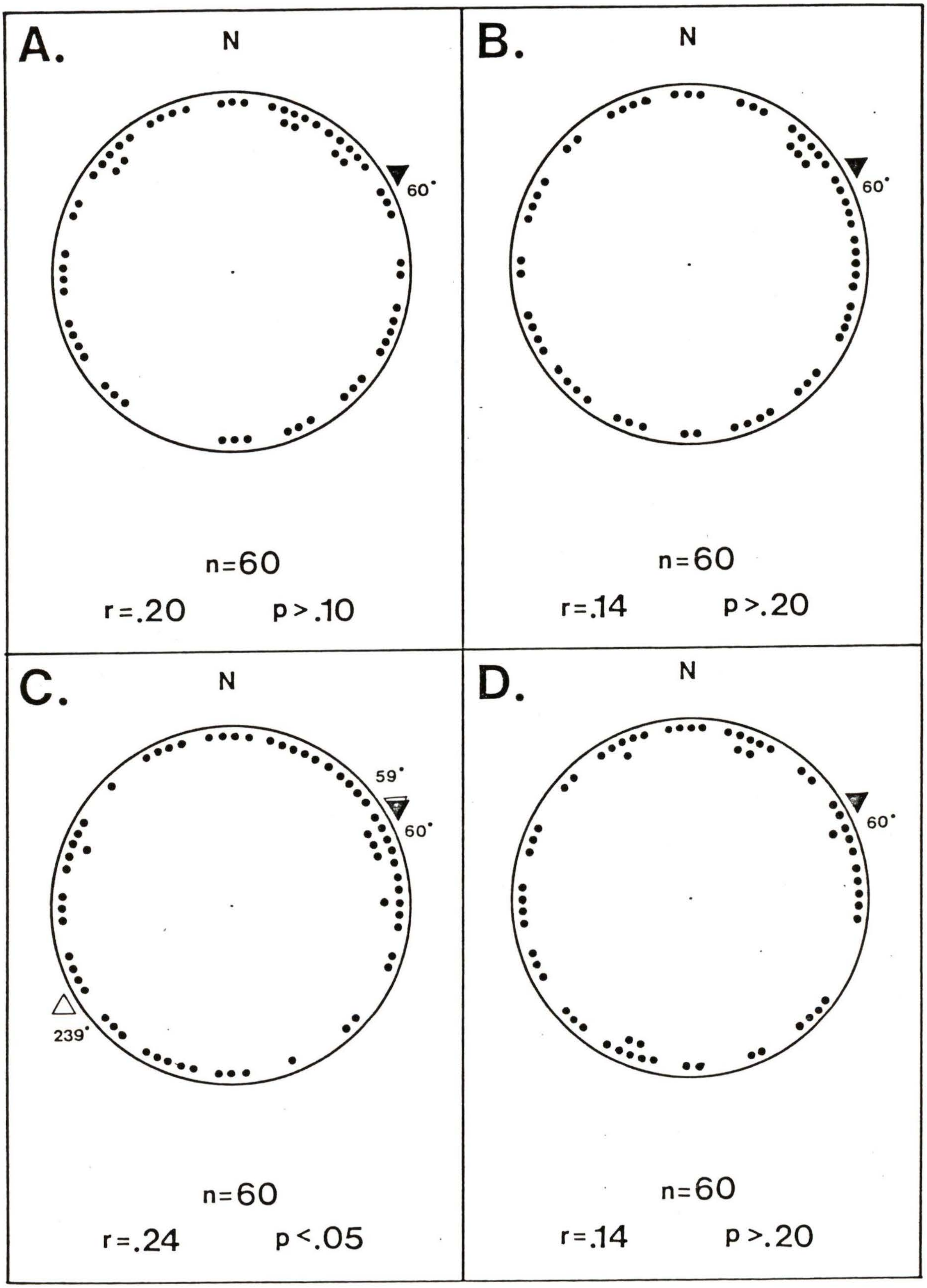
The 3 counterclockwise altered tests were all statistically significant (table 25c, fig. 33a-c). The pooled results of the 3 tests produced a highly significant mean bearing of 317°N ($p < .001$), which was not significantly different from the landward Y-axis direction of 330°N (C.I. test $p > .05$) (fig. 33d). The expected shifted direction of travel was 240°N.

To determine whether the pooled controls, clockwise altered, and the counterclockwise altered tests had significantly different mean bearings from each other, Watson-Williams analyses were conducted. The clockwise

Table 25b: Orientation of the P.B.S. beach (Y-axis = 150°N) crabs subjected to a 90° clockwise altered magnetic field. n = sample size, Y-axis and mean bearings are in °N, and p = probability.

test #	test condition	n	shifted Y-axis	mean bearing	r-value	p
131	clock. shifted	60	60	11	.20	> .10
133	" "	60	60	65	.14	> .20
134	" "	60	60	59 & 239	.24	< .05
135	" "	60	60	30 & 210	.14	> .20
clock. shifted pooled		240	60	29	.13	< .05

Figure 32. Orientation of the P.B.S. beach (Y-axis = 150°N) crabs subjected to a 90° clockwise altered magnetic field; (a-d): Tests #131, #133-#135, (e): pooled data of a-d. Legend as in fig. 6.


A.
N
60°
n=60
r=.20
p>.10
B.
N
60°
n=60
r=.14
p>.20
C.
N
59°
60°
239°
n=60
r=.24
p<.05
D.
N
60°
n=60
r=.14
p>.20

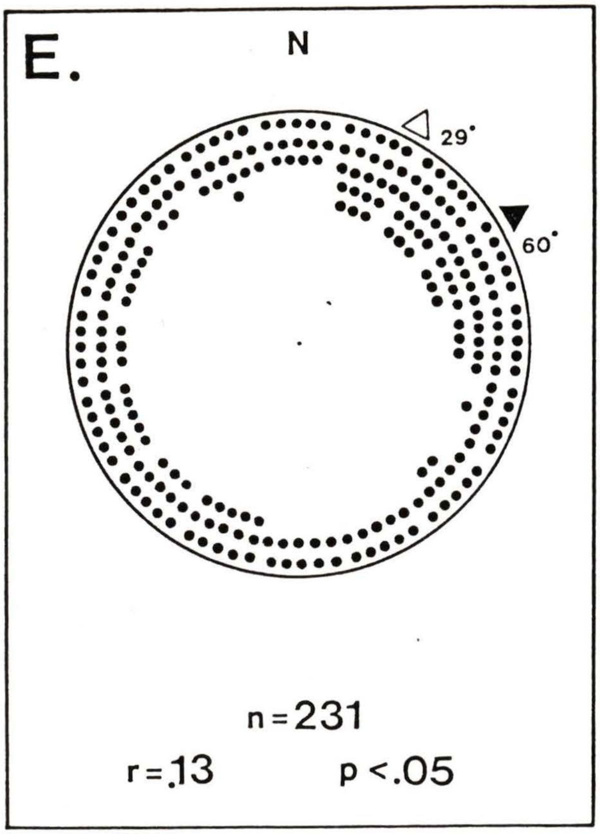

E.
N
29°
60°
n = 231
r = .13
p <.05

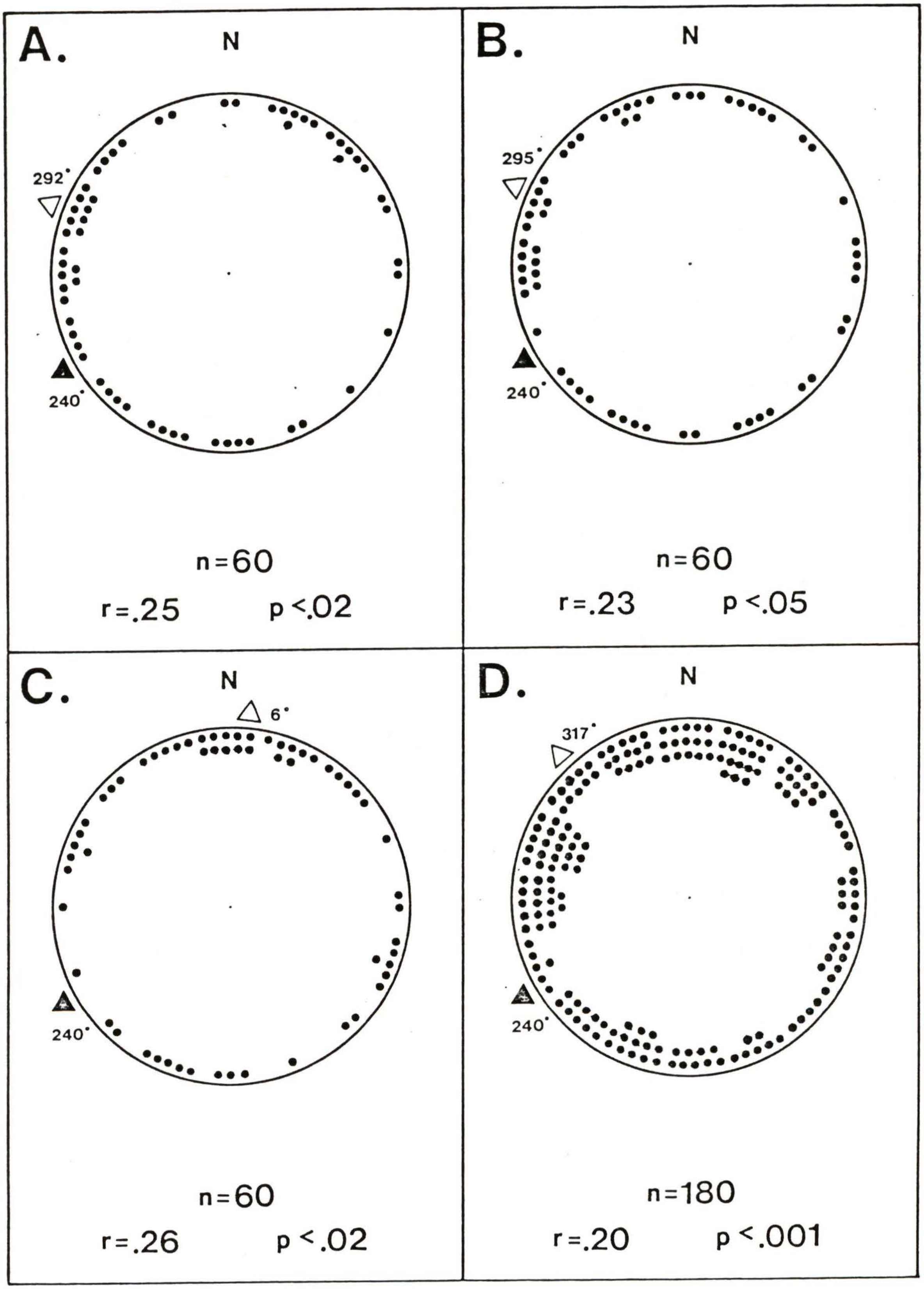
Table 25c: Orientation of the P.B.S. beach (Y-axis = 150°N) crabs exposed to a 90° counterclockwise shifted magnetic field. n = sample size, Y-axis and mean bearings are in °N, and p = probability.

test #	test condition	n	shifted Y-axis	mean bearing	r-value	p
129	countercl. shifted	60	240	292	.25	< .02
136	" "	60	240	295	.23	< .05
137	" "	60	240	6	.26	< .02
countercl. shifted pooled		180	240	317	.20	< .001

Table 26: Comparison of paired altered magnetism tests with the P.B.S. beach (Y-axis = 150°N) stock, conducted at the same time. Mean bearings are in °N.

test #	test condition	mean bearing	difference between pairs	Watson-Williams analysis
128 129	countercl.- control - shifted	289 292	- 3	p> .25
136 137	countercl.- shifted - shifted	295 6	71	p< .001

Figure 33. Orientation of the P.B.S. beach (Y-axis = 150°N) crabs exposed to a 90° counterclockwise shifted magnetic field; (a-c): Tests #129, #136, & #137, (d): pooled data of a-c. Legend as in fig. 6.


A.
N
292°
240°
n=60
r=.25 p<.02
B.
N
295°
240°
n=60
r=.23 p<.05
C.
N
6°
240°
n=60
r=.26 p<.02
D.
N
317°
240°
n=180
r=.20 p<.001

altered tests had a significantly different mean bearing (p< .001) from the control tests. A 90° clockwise shift in the magnetic N resulted in a clockwise shift of 59° in the crabs' mean bearing. The counterclockwise altered tests did not differ significantly from the control tests (p> .25), the shift being only 13° counterclockwise in the expected direction.

Significant fluctuations in the directional preference were noted in previous experiments (Chapter V). An analysis was conducted with 4 of the above tests which were performed in 2 pairs, with each pair tested at the same time to observe the effect of random fluctuations in the orientation direction (table 26).

Test #128 was a clockwise control for test #129, in which magnetic N was displaced 90° clockwise. The two tests were performed during the same testing session by turning the coil off for 5 test animals (controls, test #128) and on for the next 5 (experimentals, test #129). The Watson-Williams analysis shows that these 2 tests do not have statistically different mean bearings (p> .25) (table 26). This result is consistent with the pooled results in which the counterclockwise altered group was found not to have a significantly different mean bearing from the control group.

Two counterclockwise altered tests performed consecutively on the same day, #136 & #137, both produced significant mean bearings which were 71° apart, and which were determined to be different (Watson-Williams analysis p< .001). These results suggest that mean bearings were influenced by factors other than the magnetic field.

CONCLUDING REMARKS

The control experiments with crabs tested under the cover demonstrated that they were able to orient without sky cues. This suggested that orientation can also occur by means of non-visual cues.

I was able to show that the crabs did not orient to any feature of the testing apparatus, since any visual or non-visual directional cues derived from the position of the apparatus itself did not affect the directional preference of the crabs. It will be recalled that in order to change the magnetic N clockwise or counterclockwise, the whole cage and coil had to be rotated 90° on its long axis in the direction of the new N. The two control tests performed for each of the two different positions of the test apparatus all had mean bearings close to the expected landward Y-axis direction. If any effect of the cage position on the crabs' orientation existed, it would have manifested itself in these results.

The animals may have responded to the clockwise magnetic shift but apparently ignored the counterclockwise shift. However, the clockwise shift was only 59° in the expected direction rather than 90° as predicted. Thus the conclusions about their ability to use geomagnetic cues in orientation must remain speculative.

The two counterclockwise altered tests performed consecutively (#136 & #137) demonstrated the presence of fluctuations in the preferred direction over time. It is possible that even more radical fluctuations in the mean bearing occur over short periods of time. Large variations in the directional preference of individual crabs within any one test would be interpreted as random orientation by the circular statistics used, even if the crabs were pursuing a directional goal rather than being randomly directed. The only possible way to avoid this would be to look at directional preferences of individual crabs repeatedly retested. However, this method is considered unacceptable in this research due to its many other drawbacks such as animal fatigue and dependence of the data.

The adaptive significance of a Y-axis orientation ability by use of geomagnetic cues for *H. nudus* is potentially great. *H. nudus* populations inhabiting coastal British Columbia are subject to long periods of heavily overcast skies, especially during the winter months. Crabs displaced seaward along the substrate could only orient along the landward Y-axis by use of non-visual cues, especially if deep water obscured celestial cues and the bottom topography was variable and did not provide directional cues.

Even though these tests failed to show conclusively that H. nudus is capable of using geomagnetic cues in orientation, this ability is still highly probable for the following reasons;

1) Crabs from the Vancouver area tested in the planetarium did not respond to the altered star pattern, and yet they were able to orient along the X-axis of their home beach (Chapter VII, section 4).

2) When Nanaimo crabs were tested under a 100% overcast night sky or under cover without a view of the day sky, they oriented along the landward Y-axis of their home beach (Chapter VI).

3) A significant (Watson-Williams analysis $p < .001$) clockwise directional change of 59° was obtained with a large number of crabs ($n = 480$) to a 90° clockwise shift in the x-component of the earth's magnetic field.

Part. 4 Learning and Y-axis Orientation.

VIII. TRANSPLANT EXPERIMENTS

INTRODUCTION

The purpose of these experiments was to determine whether the Y-axis orientation in H. nudus is innate or whether it is learned by transplanting crabs from the Rocky Point (Y-axis = 330°N) to the P.B.S. beach (Y-axis = 150°N).

One of three possible results was expected. The first possibility was that the transplanted animals would change their orientation direction to that of the seaward Y-axis of the new beach; the second was that the transplanted crabs would be disoriented on the new beach; and the third was that orientation along the Y-axis of the old home beach would persist.

METHODS AND MATERIALS

EXPERIMENTAL ANIMALS

The transplant experiments were carried out between Oct. 2 - Dec. 5, 1984. A total of 600 crabs were used, 300 collected from the Rocky Point and 300 from the P.B.S. beach. The Rocky Point crabs were transported to the test facility by car in plastic buckets with lids while the P.B.S. beach crabs were carried on foot in open buckets. Prior to placement in the cages, crabs were stored indoors at the Pacific Biological Station for up to 2 days in the holding tanks with running sea water.

APPARATUS

The transplant experiments were carried out with four transplant cages. Each cage measured 60 cm in diameter and 26 cm in height. The cage frames were constructed of solid 1/4" tube aluminum and were covered with aluminum window screening (mesh size 2 X 2 mm). The screening was meshed at the seams, which were sealed with an epoxy resin. Each cage contained a removable mesh lid for access to the animals, which was fastened on the cage with locking plastic ties. The cages were constructed of non-magnetic material to prevent possible interference with geomagnetic orientation.

The cages were installed 3 m apart along the 9.2' tide line on the P.B.S. beach (Y-axis = 150°N). This tide height was chosen with respect to the proportion of time that the crabs would be exposed to air, the experimenter's access to the traps, and suitable crab habitat in the area. The test animals were collected from the same tide height locations along their home beaches.

Holes 10 cm deep were dug and the trap bottoms were sunk into them. Care was taken to ensure that the sediment layers were replaced in the bottom of the cage exactly as removed. The substrate in the cages was leveled to the height and slope of the beach substrate and was topped with rocks for the crabs to hide under. Each cage was given an identification/warning tag, and was secured to the substrate by a non-magnetic 1/8" stainless steel cable attached to an anchor ring cemented to large rocks. This was done in order to prevent removal of the cages by unauthorized persons and to prevent potential loss of cages due to rough seas or drifting logs.

The cages were kept on the beach for a period of 2 weeks prior to introduction of the crabs. This time interval allowed the substrate in the cages to unfoul and settle, allowed microscopic flaura and fauna to recolonize the cage substrate and the cage itself, and allowed any toxic manufacturing byproducts of the traps to be washed away. Since H. nudus feeds heavily on scrapings off the substrate such as diatoms and algae (Birch, 1979, Knudsen, 1964, Miller, 1980), the recolonization period was imperative to ensure a food supply for the crabs in the transplant cages.

EXPERIMENTAL PROCEDURE

Two sets of experiments were performed, each using different test animals. For the initial tests, 100 Rocky Point crabs and 100 P.B.S. beach crabs were collected. Sixty randomly chosen individuals of each population were first tested for mean directional preference in the same manner as in the first daytime tests (Chapter IV), before being placed in the transplant cages. The results of these tests were to serve as controls for comparison with results obtained at the end of the transplant study.

a) First set of transplant experiments.

The 2 populations of test crabs were marked for identification in order to distinguish them from outsiders. During the period of time that the empty cages were submerged, rips occurred due to large commercial species of crabs penetrating the mesh with their claws. Rocky Point crabs were marked with a yellow dot of Liquid Paper solution (Liquid Paper Ltd., Toronto, Ont.) applied to the median portion of the carapace, while P.B.S. beach crabs received a white dot.

The initial set of transplants consisted of randomly dividing the 100 Rocky Point crabs evenly between two cages, and the P.B.S. beach control crabs into the remaining two cages. The cages on the beach were labelled according to their position from N to S along the shoreline, namely #1N, #2N, #3S, and #4S. To avoid possible biases of beach contour and other environmental effects, the Rocky Point crabs were placed in cages #1N and #3S with the P.B.S. beach control crabs in the other 2 cages.

For the first transplant period, the Rocky Point crabs were allowed to remain in the cages for 11 days and the P.B.S. beach stock for 12 days, after which time they were retrieved and tested.

b) Second set of transplant experiments.

Due to the large loss of test crabs in this first set of experiments, a second set of tests were performed, consisting of 200 crabs from each population and placing 100 to a cage. This second set of crabs were marked in a different fashion since it was found that some of the Liquid Paper marks peeled off the crabs' carapaces during the previous test period. Both Rocky Point and P.B.S. beach crabs were marked by etching a "#" sign (about 4 mm in size) on the medio-frontal section of the carapace with a sharp razor knife. Care was taken to ensure that the etched grooves did not penetrate through the carapace and damage the crab. This more permanent method of marking could only fail if the crabs molted. However, no molting was observed during the period of testing.

For the second set of transplant experiments, the P.B.S. beach crabs were kept in the cages for 45 days and the Rocky Point crabs for 48 days. The two populations were held in the cages for slightly different lengths of time due to difficulties associated with marking and placing the 2 different populations into the cages at the same time.

RESULTS

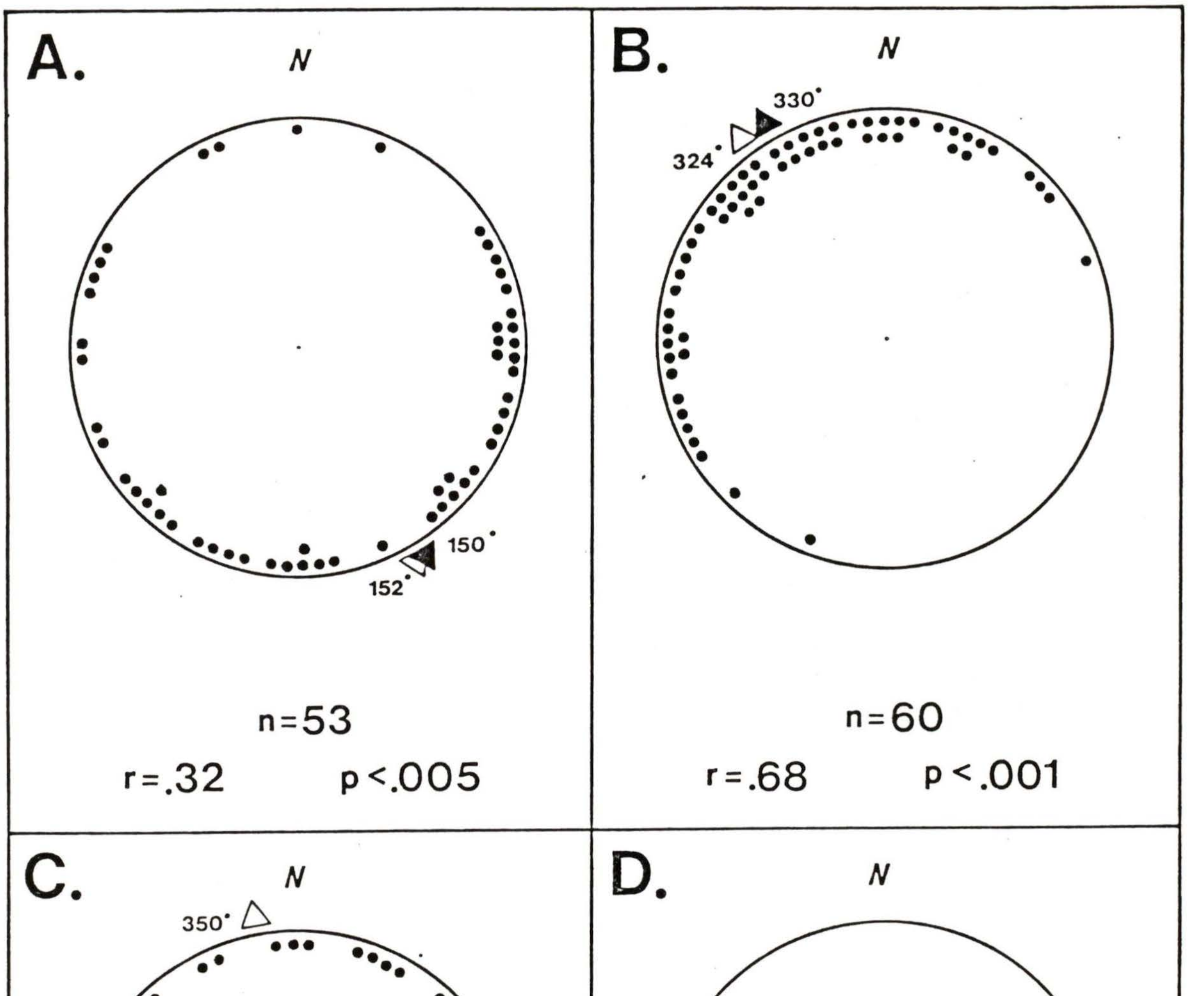
The results of the transplant experiments are presented in tables 27 & 28, and fig. 34. The 2 populations were tested at the same time by alternating the stock being tested after every 5 crabs during the same testing session. Tests #148 and #149 were the control experiments conducted with the 2 different populations prior to their placement in the transplant cages. Sixty Rocky Point and 53 P.B.S. beach crabs were randomly selected and tested from the 2 populations of 100 crabs each used in the transplant. Test #148 with the P.B.S. beach control crabs showed a mean bearing of 152°N ($p < .005$), along the P.B.S. beach seaward Y-axis direction of 150°N (C.I. test $p > .05$) (table 27, fig. 34a). Test #149 with the Rocky Point stock had a mean bearing of

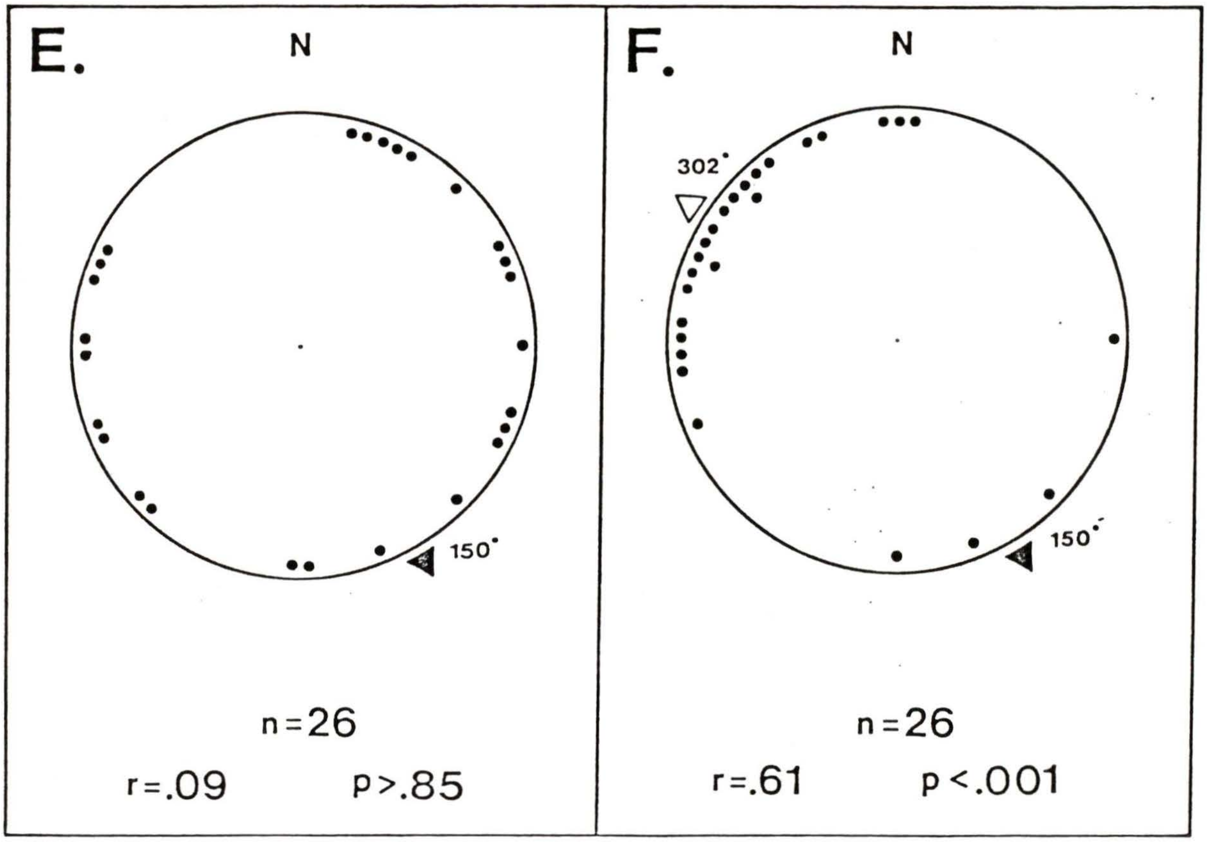
Table 27: Orientation results of the first transplant experiment with the Rocky Point (Y-axis = 330°N) crabs transplanted to the P.B.S. beach (Y-axis = 150°N). Expected and mean bearings are in °N, and p = probability.

test #	crab stock	total # crabs transplanted	days down	# crabs recovered	% overcast
148	P.B.S. beach	100	0	53 tested	45
149	Rocky Point	100	0	60 tested	45
164	Rocky Point	-	11	22	10
165	P.B.S. beach	-	12	7	10

test #	expected direction	mean bearing	r-value	p
148	150	152	.32	< .005
149	330	324	.68	< .001
164	150 or 330	350	.51	< .005
165	150	162	.31	> .50

Figure 34. Orientation results of transplant experiments with the Rocky Point (Y-axis = 330°N) crabs transplanted to the P.B.S. beach (Y-axis = 150°N). First set of tests; (a): Test #148, P.B.S. beach control stock, and (b): Test #149, Rocky Point stock, were conducted before placing crabs in cages, (c): Test #164, Rocky Point crabs after 11 days in cages, (d): Test #165, P.B.S. beach control crabs after 12 days in cages. Second set of tests; (e): Test #181, P.B.S. control crabs after 45 days in cages, and (f): Test #182, Rocky Point stock after 48 days in cages. Legend as in fig. 6.


A.
N
150°
152°
n=53
r=.32
p<.005
B.
N
330°
324°
n=60
r=.68
p<.001
C.
N
350°
150°
n=22
r=.51
p<.005
D.
N
150°
n=7
r=.31
p>.50


E.
N
150°
n=26
r=.09
p>.85
F.
N
302°
150°
n=26
r=.61
p<.001

324°N ($p < .001$), which was along the Rocky Point seaward Y-axis direction of 330°N (C.I. test $p > .05$) (table 27, fig. 34b). Thus both stocks produced highly significant mean bearings along the seaward Y-axes of their home beaches.

The crabs were tested under a 20% overcast day sky, with the sun fully visible for the duration of the testing period. The mean orientation of the 22 Rocky Point crabs remaining after 11 days in the transplant cages was 350°N ($p < .005$) (test #164). This bearing was not significantly different from the seaward Y-axis direction of 330°N of the Rocky Point crabs' original home shore (C.I. test $p > .05$) (table 27, fig. 34c).

The P.B.S. control group was reduced to only 7 identifiable individuals after being in the cages for 12 days. Although the crabs were reasonably well oriented ($r = .31$, table 27, fig. 34d), the small sample size of 7 crabs which scored in test #165 was not sufficient to produce a significant result ($p > .50$). The mean direction of 162°N, however, was close to the seaward Y-axis direction of the P.B.S. beach (fig. 34d). I conclude that the Rocky Point population did not adjust their seaward Y-axis orientation direction to that of the new beach within 11 days after being transplanted. They persistently oriented along the seaward Y-axis direction of the home beach from which they were collected.

In order to find out if the orientation of the Rocky Point transplanted crabs changes after a longer period of time, a set of long term experiments were conducted with 200 Rocky Point transplanted crabs and 200 P.B.S. beach resident (control) crabs. The results are presented in table 28.

The crabs were not tested prior to placement in the cages. Due to severe cage destruction by large crabs, only 26 crabs were recovered of both the P.B.S. beach and Rocky Point populations. The P.B.S. beach crabs oriented randomly after 45 days in the cages ($p > .85$) (test #181, table 28, fig. 34e). The Rocky Point crabs were tested after 48 days down, at the same time as the P.B.S. controls (test #182). These crabs showed a

Table 28: Orientation results of the second transplant experiment with the Rocky Point (Y-axis = 330°N) crabs transplanted to the P.B.S. beach (Y-axis = 150°N). Expected and mean bearings are in °N, and p = probability.

test #	crab stock	total # crabs transplanted	days down	# crabs recovered	% overcast
181	P.B.S. beach	200	45	26	50
182	Rocky Point	200	48	26	50

test #	expected direction	mean bearing	r-value	p
181	150	73	.09	> .85
182	150 or 330	302	.61	< .001

highly significant mean bearing of 302°N ($p < .001$), which was only in the general seaward Y-axis direction of the original home beach (330°N) (C.I. test $p < .05$) (table 28, fig. 34f). From the orientation of the transplanted crabs, I conclude that the Rocky Point stock did not change their orientation direction even after 48 days on the new beach. They consistently oriented in the seaward Y-axis direction of their original Rocky Point home beach.

CONCLUDING REMARKS

The transplanted crabs did not change their Y-axis orientation direction to the new beach. This suggest three possibilities for the observed orientation; 1) it is innate, or 2) it is learned early in development and does not change later in life (like imprinting), or 3) the transplant cages interferred with the relearning process.

Innate orientation perpendicular to the land-water interface is commonly associated with beach-dwelling animals which do not freely disperse their offspring into the water. For example, innate orientation is found in littoral amphipods such as Talitrus saltator, Talorchestia deshayesei, and Orchestia mediterranea, which raise their offspring in their brood pouch (Pardi, 1960; Pardi and Scapini, 1983; Scapini and Pardi, 1979; Scapini et al., 1985), and shore-dwelling wolf spinders, Arctosa sp., which raise their young on the parent's body, rather than dispersing them into the environment. The innate Y-axis orientation in these species is modifiable by later experiences (learning).

Innate orientation in a specific direction by H. nudus larvae would necesitate one of at least 2 prerequisites. One is that H. nudus do not have freely planktonic larvae which are dispersed into the environment after the eggs hatch, as is commonly assumed (Hart, 1982). Rather, the swimming larvae would stay in close proximity to their home beach (in spite of current) and later settle on it. However, it is unlikely that the larvae would be able to orient in tidal currents, and thus their movement in the water would make innate orientation maladaptive.

An innate mechanism could also function in crab larvae which are freely planktonic but somehow later manage to locate and settle on beaches with an orientation simmilar to the home beach of the parent population. This ability would require some sort of directional orientation or perhaps homing by the larve. J. Booth (unpubl. data) performed orientation experiments with Cancer magister megalope collected from the mouth of Gray's Harbor estuary in Washington state. The results were indicative of a landward orientation towards shallow waters of the bay, where the magelope settle and metamorphose into the adult form. Whether a similar orientation by H. nudus larvae occurs is not known.

If the crabs learn the Y-axis direction of the beach that they settle on, this direction could be learned after metamorphosing and settling on the beach during an early "imprinting" period. Ferguson and Landreth (1966) suggested that in Fowler's toads, Bufo fowleri, the Y-axis may be imprinted early in life and retained. H. nudus as small as 1.00 cm perform Y-axis orientation, suggesting that learning must occur before this size is reached.

It is unlikely that the transplant period was not sufficiently long to produce relearning. If a Y-axis orientation response is necessary to the animals' survival, a crab disoriented on an unfamiliar beach would likely perish within a few hours or days.

It is possible that the holding cages somehow interfered with modification of the orientation response, since the P.B.S. beach control crabs were unable to orient in test #181, after being held in the cages for 45 days. To learn a new Y-axis direction, the crabs may have to be able to freely travel along the beach. A greater freedom of movement could be accomplished by using a mark-recapture method or constructing larger cages for the transplanted animals. However, why would the cages only affect the orientation strength of the P.B.S. beach and not the

Rocky Point stock?

The method used for marking the crabs also deserves some attention. I developed what I believe to be a good, semi-permanent method of marking small crabs by etching their carapace. This method is suitable for long-term marking of *H. nudus* for the following reason. The original Rocky Point crabs in the cages could be easily distinguished from P.B.S. beach crabs which invaded the cages, not only on the basis of their tags but also by body color. The Rocky Point crabs are a darker purple color, and almost devoid of green markings, while the P.B.S. beach crabs are heavily covered in green markings. No dark purple crabs without etched markings were found in the cages. From this I conclude that etching the carapace is an effective method of marking *H. nudus* between molts.

IX. GENERAL DISCUSSION

I have experimentally shown in this study that *H. nudus* could accurately determine Y-axis directions with respect to the shoreline. Contrary to the Bamfield and Nanaimo crabs which perform Y-axis movements, the Vancouver crabs in these experiments demonstrated X-axis orientation.

The occurrence of Y-axis movements under natural circumstances was also observed in crabs of the Rocky Point shoreline during mid-ebb and mid-flow tides under sunny, low overcast conditions. Two-meter transects were established parallel to the shore at the land/water interface, and the number of crabs crossing the transect in either direction were scored during 5 min intervals. Under flow tide conditions, a total of 719 crabs in 11 transects were recorded heading landward, while none moved seaward. During ebb tide, 218 crabs in 24 transects headed seaward and none landward. Thus under natural conditions, these crabs make landward and seaward migrations with respect to the tidal cycle.

Shore-dwelling crustaceans often show oriented movements along the X- or Y-axes. Y-axis movements under natural conditions most commonly represent upshore and downshore zonal migrations in response to tide levels. They are often interpreted as resource aquisition movements, for commodities such as moisture, food, conspecifics, and habitation (Herrnkind, 1983). The adaptive significance of such an orientation system may however also be related to predator avoidance. *H. nudus* is preyed upon aerially by avian predators and underwater by a host of fish and larger crabs. The optimal escape reaction of the crabs would be to the shallow water near the land-water interface, which the predators can not enter.

It is possible that the Vancouver Island and Mainland crabs have aquired or developed the different types of shore-directed orientation in order to achieve the same goal. The 2 populations may be thought of as biotypes which have most likely been isolated from each other for a sufficiently long period of time to develop different survival strategies. Alternatively, all populations may have the capability to orient in various manners, but respond in a particular fashion as determined by local environmental factors.

The Y-axis directional preference was found to be independent of crab sex and size, and a variety of environmental factors such as tidal, diel, observer, temperature, and lunar effects. It was only affected by clear sky blockage and light intensity changes. However, the Y-axis orientation ability was found to vary between tests, even when these were conducted consequitively under the same experimental and environmental conditions. The differences in individual responses affected the mean bearing for the particular test. As Adler and Taylor (1981) pointed out, the observed variability in directional preference among the tests may have been due to either 1) a random deviation of each individual crab's bearing from the group mean bearing, or to 2) individually consistent bearings which deviated in some constant way from the group mean. The latter situation would indicate that individuals orient more precisely than the pooled results suggest. Repetitive testing of the same individuals to determine these effects was not within the scope of this research.

The question arises as to the importance of orientation cues tested under experimental conditions to crabs in the wild, where orientation by use of other orientation mechanisms may be involved, especially in close proximity to home. It is likely that proximal cues in a natural situation (such as landmarks and slope of substrate) are important as guiding mechanisms for orientation in H. nudus. However, the crabs were able to use other orientation cues under experimental conditions even when displaced large distances from their home environment, suggesting that the orientation cues tested for must have some ecological value.

Several orientation systems may be functional under experimental conditions, and various orientation cues may be chosen by H. nudus during different environmental conditions. Meteorological conditions, experience, and physiological state of the animal are factors that may govern the relative importance of a number of cues in providing usefull directional information (Ferguson and Landreth, 1966).

When several different types of orientation cues are available, it is unlikely that the crabs would rely only upon one sense rather than a multiple sensory input. The availability of visual cues such as the sun, polarized light, stars, and the moon exists in a continuum with periods of transition during which the types of cues change during the diel cycle. It is likely that during these periods an overlap in the use of directional cues exists.

Orientation by the use of visual cues requires 3 sources of information; 1) a learned or innate knowledge of the compass direction of the shoreline, land and water 2) a reference to a directional cue(s) (visual in this case), and 3) local time provided by an internal clock phased to compensate for the apparent movement of the celestial directional cues. Crabs which were provided with this type of information in the early tests (Chapter IV), were well oriented.

Visual nighttime orientation cues consist of the moon and stars, but it was determined with the P.B.S. beach and Rocky Point stocks that the presence of the moon was not necessary for correct orientation at night. It was determined from the planetarium results, that the importance of stars as orientation cues is also minimal. These results indicate that the crabs did not orient on the basis of visual orientation cues at night. This is understandable since dependence on the moon or stars to provide directional cues would not be adaptive during 1) the phase of the new moon when it is not visible at all and 2) when clouds obscure the celestial cues. During these periods, a non-visual system provides the only reliable directional cues.

Tests conducted under overcast skies (Chapter VI), under cover in altered or unaltered magnetic fields (Chapter VII), and in the planetarium (Chapter VII), suggest that a backup system based on non-visual cues, most likely geomagnetism, becomes important during these times. Orientation by use of non-visual cues, namely geomagnetism, is simplified. No internal clock is required since no large daily or seasonal shifts exist in the magnetic field through time.

Such a system may ensure survival under a variety of environmental conditions, and is potentially useful under any weather conditions. However, crabs which appeared to orient by non-visual magnetic cues oriented more weakly than those presented with clear sky cues, suggesting that a visual orientation system provided more accurate directional information to the crabs. Why a visual orientation system provides for a seaward orientation while a non-visual one provides for a landward orientation is unknown.

Animals presumably can not see the sun as a discreet light source when tested under cloud cover or when the sun is experimentally blocked from view. Under these conditions, polarized light is also absent, which implies that any directional orientation at this time is based on non-visual cues. However, it should be noted that Verheijen (1978) proposed that the remaining anisotropy of the radiance field (anisotropic radiance distribution or ARD) may also serve as a directional cue, due to the vectorial parameter of the radiance field. Van Rhijn and Van Gorkom (1983) demonstrated that the ARD is used at night in sea-finding orientation in sea turtles (*Chelonia mydas*), and Herrnkind (1983) suggested the orientation of fiddler crabs (*Uca* sp.) may be affected by the ARD during daytime testing. Enright (1972) even noted that Talitrid amphipods may use the ARD of moonlight in night orientation when the view of the moon is blocked. Orientation to this type of visual cue by *H. nudus* was not tested due to the difficulties associated with quantifying the ARD.

A non-visual system is not restricted by meterological conditions, and is thus potentially available all of the time. However, the visual system seems dominant, since it was the only one manifested when sky cues were present. The non-visual system can however be immediately adopted when the animals are placed under cover. If Y-axis orientation is necessary for individual survival in *H. nudus*, then use of non-visual orientation cues under certain environmental conditions would be adaptive. Use of these cues would seem indispensable for *H. nudus* populations living on coasts of B.C. due to the long periods of heavily overcast skies that frequent the area, especially during the winter months.

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Appendix

TERMINOLOGY

celestial - referring to bodies present in the sky; sun, moon, planets, and stars.

day, daytime - a period of the diurnal cycle between sunrise and sunset.

directional preference - the mean bearing taken by an individual or group, when the directional distribution is significantly different from uniform.

e-vector - plane of light polarization.

home beach - the proximal familiar intertidal area from which the crabs were collected.

homing - navigating to a specific area or location which is regarded as home.

innate - behavioral differences between individuals or populations not affected by the environment during ontogenic development.

internal (biological, endogenous) clock - animals possess a fully self-contained means which provides local time and is used for measuring closely the durations of natural geophysical periods (such as the solar day).

navigation - the animals know where they are and where their destination is, and are able to set a bearing toward the destination.

night, nighttime - that period in the diurnal cycle between sunset and sunrise.

orient(ation) - an ability of the animals to pursue a given compass direction in the horizontal plane without reference to landmarks, when released in an unfamiliar territory (Able, 1980).

stellar - referring to stars only.

sun-compass - the position of the sun is used for orientation and is coupled with the internal circadian rhythm (clock) of the animal to compensate for the apparent movement of the sun across its daily arc (Grier, 1984).

X-axis - the 2 directions parallel to a shoreline.

Y-axis - the 2 directions perpendicular to a shoreline (X-axis) (Ferguson and Landreth, 1966).

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