ZOOGEOGRAPHIC PATTERNS OF IDOTEID ISOPODS IN THE NORTHEAST PACIFIC, WITH A REVIEW OF SHALLOW WATER ZOOGEOGRAPHY OF THE AREA

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Abstract.—The northeast Pacific coastal region (equator to central Alaska), is one of meterological and hydrographic variability, particularly in southern California and northwestern Mexico, where monthly, yearly and long-term cyclic fluctuations in water temperature are the rule. Delineation of coastal biogeographic provinces there is problematic because of hydrographic variability, and because eurythermy, long-term temperature acclimation, and various types of compensatory metabolic changes occur in a variety of the indigenous invertebrates.

The isopod family Idoteidae is a cool to cold water centered group, but several shallow water genera penetrate into the warm subtropical waters of western Mexico. *Synidotea* and *Saduria* are essentially restricted to the Arctic, Aleutian and Oregonian Provinces; *Edotea* occurs in the cold and warm temperate (Oregonian and Californian) provinces; *Erichsonella* and *Colidotea* occur in the California-Cortez Provinces; *Cleantis* and *Eusymmerus* are strictly tropical/sub-tropical; but *Idotea* ranges through five provinces (Arctic to Cortez). Although isolated reproducing populations of certain species of *Idotea* occur south of their principal range, significant populations are not maintained in these warmer waters. *I. urotoma* can acclimate to, and apparently reproduce in, experimental temperatures of 28°C. At ambient sea water temperatures (ca. 20°C) its critical thermal maximum (CTMx) was 34°C; at 27°C acclimation temperature, CTMx was 40°C. These tolerances are consistent with mean and maximum onshore water temperatures in northwestern Mexico, and suggest that the primary factor limiting southern distribution of *Idotea* may not be temperature.

Species of *Idotea, Colidotea, Erichsonella* and *Eusymmerus* show a strong preference for living upon laminarian algae which they use for substrate and food. The southern distributional limit of *Idotea* coincides with that of their preferred brown algae, and also with the northernmost occurrence of *Colidotea, Erichsonella* and *Eusymmerus*. Latitudes at which this ecological replacement takes place coincide with the California-Cortez Transition Zone, a region of considerable species diversity. The southern limit of some species of northeast Pacific *Idotea* may be regulated primarily by biotic factors: 1) competition by tropical genera of algal inhabiting idoteids; 2) predation by tropical fishes; 3) lack of suitable algal substrate.

ЗООГЕОГРАФИЧЕСКИЕ МОДЕЛИ РАВНОНОГИХ IDOTEIDAE
В СЕВЕРО-ВОСТОНЧОЙ ЧАСТИ ТИХОГО ОКЕАНА
С ОБЗОРОМ ЗООГЕОГРАФИИ НЕГЛУБОКИХ ВОД РАЙОНА

Реферат.--Северо-восточный прибрежный район Тихого океана
/от экватора до центральной Аляски/ отличается неустойчивостью
метеорологических и гидрографических условий, особенно в южной
Калифорнии и северо-западной Мексике, где ежемесячные, ежегод-
ные и долгосрочные циклические колыбания температуры воды явля-
ются.правилом. Трудно установить прибрежные биогеографические
провинции из-за гидрографической неустойчивости; эвритермия, дол-
госрочная температурная акклиматизация и различные метаболические
изменения относятся к различным местным беспозвоночым.

Семья равноногих Idoteida - группа, которая концентрируется
в прохладной и холодной воде, но несколько родов - в неглубоких
водах проникают в теплые субтропические воды западной Мексики.
Synidotea и *Saduria* в основном находятся только в Арктической,
Алеутской и Орегонской провинциях; *Edotea* - в холодных и теплых
провинциях /Орегонской и Калифорнийской/; *Erichsonella* и *Colido-*
tea в Калифорнийско-Сортезских провинциях; *Cleantis* и *Eusymmerus* -
исключительно тропические/субтропические; *Idotea* - в пяти про-
винциях /от Арктической до Кортезской/. Хотя отдельные воспро-
изводящиеся популяции некоторых видов *Idotea* встречаются на юге
от основного распределения, значительные популяции не поддержи-
ваются в этих более теплых водах. *I. urotoma* способен акклима-
тизироваться, и кажется, размножается в опытной температуре 20°С.
При температуре окружающей морской воды /са. 20°С/ его критический
тепловый максимум /CTMx/ - 34°С; при температуре акклиматизации
27°С - CTMx - 40°С. Эти величины, представляющие толерантности,
соответствуют средней и максимальной температуре прибрежной воды
в северо-западной Мексике. Возможно, что температура не является
основным фактором, ограничивающим южное распространение *Idotea*.

Виды *Idotea, Colidotea, Erichsonella* и *Eusymmerus* предпочи-
тают жить на ламинариевых водорослях, которые используются ими в
роли субстрата и пищи. Южная граница района распространения
Idotea соответствует границе предпочитанной ими бурой водоросли,
к тому же, найболыше к северу выдвинутой грайнице распространения
Colidotea, Erichsonella и *Eusymmerus*. Широты, где происходит
это экологическое замещание соответствуют Калифорнийско-Кортез-
ской переходной зоне, каторая отличается значителььчым разнообра-
зием видов. Южная граница некоторых видов *Idotea* северо-восточ-
ного Тихого океана в основном регулируется биотическими фактора-
ми: 1/ конкуренцией со стороны тропических родов *Idotea* живующих
на водорослях; 2/ хищной активностью тропических рыб; 3/ отсутст-
вием подходяшего водорослевого субстрата.

Introduction

Environmental temperatures have long been accepted as playing the pre-
dominant role in regulating the distribution of animal species. Our purpose
in this paper is to present a review of the current literature (primarily 1965
to present) dealing with relevant oceanographic features of the northeast
Pacific, and the role of temperature in the regulation of animal distribution
in the nearshore waters. We present preliminary data that suggest temper-
ature is *not* regulating the southern distributional limits of certain idoteid

isopods. These preliminary data are of two kinds, distributional (collection) records and laboratory experimentation. In conclusion we offer the hypothesis that biotic factors are primarily responsible for the regulation of latitudinal·distribution in certain species of shallow water Idoteidae.

1. Marine Biogeography on the Northeast Pacific coast—an overview.— The concept of global circulation of air masses controlled by temperature differentials is a well understood meteorological phenomenon (see, for example, Borchert 1953 and Bryson 1966). Local climatological effects of this system are easily measurable. The long-range effects of movements of air masses influence the world's seas both directly (e.g., waves, oceanic circulatory patterns, broad scale thermal regulation, etc.), and indirectly (e.g., localized elevations or depressions in sea level, upwellings, transport of airborne particulate matter, rainfall and runoff, etc.). The effects of these atmospheric influences on the world's seas are not always immediately clear, and in many cases only partly understood. It is far easier, for example, to measure currents and water temperature at a point in time and space, than it is to produce a model that can explain why such conditions exist; or, that can predict such conditions (Parsons 1976). A classic example of this problem in integration is the El Niño system of the central southeast Pacific (Fig. 1) which has only recently begun to be described in terms of cause-effect relationships (see: Wyrtki 1965a, 1966; White and McCreary 1974; Bjerknes 1961; Wyrtki et al. 1976; and others). These problems are multiplied in coastal situations and in meteorologically complex localities, one of which is the Pacific coast of North America. Figure 1 gives an overview of oceanic circulatory patterns in this region.

Some of the important phenomena that disrupt the generalized patterns seen in Fig. 1, and produce a more heterogenous and often unpredictable environment in this region are: (1) the west coast of the United States and Baja California (Mexico) is one of the world's major regions of upwelling; (2) the coastal southern extent of the California Current is a variable feature, largely unpredictable, which south of 30°N latitude becomes a wide slow drift strongly influenced by localized disturbances (e.g., upwellings, winds, coastal topography, etc.); (3) much of the coast consists of alternating areas of cold upwelling waters and warm shallow bays and lagoons, especially between Point Conception (California) and Cabo San Lucas (Baja California); (4) much of the coast of southern California and west Mexico is under the influence of complex, nearshore, seasonal currents and local eddy systems (Wyrtki 1965b, summary); and (5) the relatively warm, northward flowing subsurface Davidson current surfaces in winter and appears to "push" the colder, southward flowing California Current offshore. The Davidson is a highly variable current, both in strength and duration. It usually begins somewhere near the southern tip of Baja California and may extend as far north as Vancouver Island. Griggs (1974) examined these alternating cur-

Fig. 1. General patterns of oceanic circulation in the east Pacific Ocean.

rents in some detail in central California, reporting northward winter speeds of 3 to 11 km/day for the Davidson Current, and southward spring speeds of 4 to 10 km/day for the California Current. Drift in this region during summer and fall is variable, with occasional reversals of direction partly associated with eddies of the California Current system as well as local wind patterns.

The California Current is comprised of a complex pattern of meandering and changing water flows. From central California south, the integrity of this current declines, and in southern California a large eddy is usually present on the eastern boundary, creating a nearshore north-flowing countercurrent. The strength of this countercurrent is enhanced by the rise of the Davidson Current in the winter. Only from March to May does a nearshore current flow southeast the entire length of the Baja Coast. The remainder of the year, the main current moves offshore and a complex series of eddies develop along the coast, the largest of these being the one just south of Punta Eugenio. North of Punta Eugenio winds generally blow from the NW or NNW throughout the year, creating an intense semi-permanent upwelling just north of this large promontory. Between Cabo San Lucas, Cabo Corrientes and the Islas Revillagigedos is a region of strong convergence, where three water masses meet (the California Current, north flowing equatorial waters, and Gulf of California water).

The entire eastern Pacific coastal region, particularly south of Point Conception (California) is marked by changing temperature and salinity gradients and inversions (see: Cromwell and Reid 1956; Roden 1959, 1961, 1972; Arthur 1960; Sette and Isaacs 1960; Stewart 1960; Griffith 1963, 1965, 1968; Carsola et al. 1965; Cairns and LaFond 1966; Cairns 1966, 1968; Carsola 1967; Lynn 1967; Saur and Stewart 1967; Cairns and Nelson 1970; Stevenson 1970; and Warsh and Warsh 1971). For a discussion of variations in water masses along the Oregon-California-Baja Coast, see Fleming (1940), Reid et al. (1958), Emery (1960), Shepard (1960), Gaul and Stewart (1960), Reid (1960, 1962), Wooster and Reid (1963), Schwartzlose (1963), Wyrtki (1965b), Gleason (1966), Pavlova (1966), Wyllie (1966), Lynn (1967), Wooster and Jones (1970), J. H. Jones (1971), Bakun et al. (1974), and Bourke and Pattullo (1974). In addition to local heating and upwelling phenomena, river runoff plays an important role in modifying local conditions sporadically throughout the Pacific Northwest (Conomos and Cross 1968; J. H. Jones 1971; Royer 1975; Bakus in press; and Brusca and Brusca 1978).

These, and other phenomena, all result in a coastal region that is oceanographically and climatologically complex, and one that experiences considerable variability in water temperatures. As instructors each spring at the University of Southern California's Catalina Marine Science Center, the authors have observed the influence of these thermal fluctuations in changing the composition of local shallow water invertebrate communities. As

mean water temperatures have increased regularly from 1975 to 1977, the Davidson Current has carried increasing numbers of viable subtropical animals northward.

Despite these variable coastal conditions, a generally agreed-upon system of classifying the northeastern Pacific coast has evolved over the past 13 decades (Woodward 1851–1856; Dana 1853; Forbes 1856; Gunter 1880; Ortmann 1896; Bartholomew, et al. 1911; Ekman 1935, 1953; Schenk and Keen 1936, 1937, 1940; Newell 1948; Valentine 1966; Brusca 1973, 1979; Briggs 1974; and, Hayden and Dolan 1976). This system is presented in Fig. 2. Although its foundations have been attributed to a number of different workers, the essential features date back to Dana's (1853) impressive monograph on the geographical distribution of Crustacea. Dana used, as the basis of his zoogeographic scheme, *isocrymal lines* (i.e., mean surface water temperature for the coldest 30 consecutive days of the year). Clearly, he considered lower thermal tolerance levels to be of prime importance in limiting the distribution of marine Crustacea.

The regions shown in Fig. 2 are as follows: North of the Bering Strait is the POLAR or FRIGID ZONE, wherein water temperatures are generally near or below 0°C year around. From the Bering Strait south to about Point Conception (California) is the COLD TEMPERATE ZONE, where minimum winter water temperatures rarely drop below 0°C, and maximums rarely exceed 20°C. From Point Conception south to the west coast of Baja California (Mexico) is the WARM TEMPERATE ZONE, where water temperatures rarely drop below 10°C, or exceed 25°C.[1] From Baja California south to about 16° north latitude is the SUBTROPICAL ZONE, where winter water temperatures rarely drop below 13–15°C, but summer temperatures may rise to 25°C or 30°C. Below this lies the TROPICAL ZONE, where winter water temperatures rarely drop below 18–20°C. These figures are generalizations and localized perturbations of the northeast Pacific coastal environment are the rule rather than the exception. It is these variable conditions that are no doubt responsible, in part, for the wide thermal tolerances seen in many groups of temperate coastal marine invertebrates. Within the temperate and subtropical/tropical coastal zones, as here defined, the overall temperature range of the former always exceeds that of the latter by a considerable margin. Unfortunately, few data are available for onshore (intertidal and shallow subtidal) water temperatures for much of the northeast Pacific, particularly south of the U.S.-Mexican border. The majority of published temperature data have been collected from oceanographic ships, considerable distances offshore (for example, Robinson's [1973] excellent compendium in which 35,804 bathythermograph and reversing thermometer observations were integrated to produce computer plots of monthly isotherms for both coasts of Baja California).

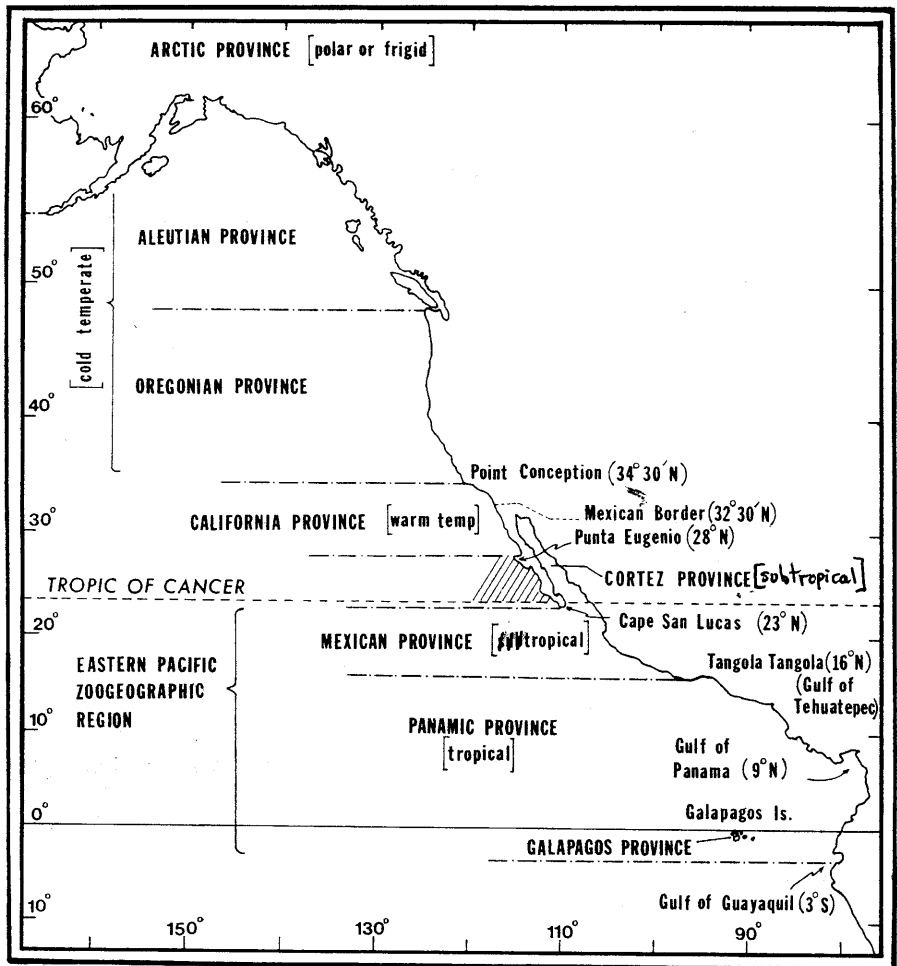These "thermal zones" have also been characterized by their faunal and

Fig. 2.   Shallow water zoogeographic provinces of the northeast Pacific.

floral components, in particular the molluscan fauna. Valentine (1966) pre-
sented a brief historical review of the various provincial systems that have
been proposed for the Mollusca, and pointed out that distributional patterns
of shallow water benthic molluscs have served as the primary basis for the
delineation of marine faunal provinces in the eastern north Pacific for over
a century. Valentine (1966), Briggs (1974) and Brusca (1979) gave reviews
and literature citations for most of this work, virtually all of which ap-
proached the problem on a species-by-species level, rather than the com-
munity level approach taken by some workers with regard to the sublittoral
and deep benthic fauna (see Thorson 1957, and Parsons et al. 1977). The

biogeographic terms that are presently applied to these regions are also presented in Fig. 2: the polar zone is usually referred to as the ARCTIC PROVINCE; the cold temperate zone is generally divided into a northern ALEUTIAN PROVINCE and a southern OREGONIAN PROVINCE (the division between these two usually being placed at about the Strait of Juan de Fuca); and, the warm temperate zone is referred to by most modern workers as the CALIFORNIAN PROVINCE, but by ichthyologists as the SAN·DIEGAN PROVINCE. The subtropical-tropical region was split into four provinces by Briggs (1974): the CORTEZ PROVINCE (the Gulf of California); the MEXICAN PROVINCE (south to the Gulf of Tehuantepec, Mexico—possibly derived from Dana's original nomenclature); the PAN-AMIC PROVINCE (restricted to the easten Pacific tropics south of about 16°N latitude); and the Galapagos Islands designated a separate GALA-PAGOS PROVINCE within the eastern Pacific tropics. The Cortez, Mexican, Panamic and Galapagos Provinces are collectively referred to as the EASTERN PACIFIC ZOOGEOGRAPHIC REGION[2]—a somewhat misleading term meant to include the warm (non-temperate) waters of this region. The degree of endemism within the Eastern Pacific Zoogeographic Region is very high in all groups except the bryozoans, the polychaete superfamily Eunicea, and perhaps the sponges. As Fauchald (1969) pointed out, the apparent lack of endemism in these groups may be due to insufficient taxonomic data on them.

Hall (1960, 1964) noted the existence of several recognizable molluscan assemblages within the Oregonian Province, as did Valentine (1966). The southern Oregonian assemblage was designated the Montereyan Subprovince by Hall, a term perpetuated by Valentine. Valentine designated the central region as the Mendocinan Subprovince, the northern as the Columbian Subprovince. The latter was based on the somewhat distinct shelled molluscan assemblage of the Puget Sound to Dixon Entrance area, a phenomenon perhaps first recorded by Woodward (1851–1856). The transition between the Arctic and Aleutian Provinces is a gradual one and various authors have placed the division at the Bering Strait, Kodiak Island, the Pribilof Islands, and Kotzebue Sound. Bakus (pers. comm.) has recorded sea surface temperatures as high as 12°C in the Bering Sea, and 16°C in the Gulf of Alaska.

Although this system seems to well serve its purpose, numerous problems exist, both in terms of water temperatures conforming to particular biogeographic provinces, and in terms of the extended or discontinuous ranges of many shallow water taxa, and it seems apparent that faunal provinces on the west coast of North America are not nearly as discrete as those of the east coast. This is likely to be part of a world wide pattern resulting from the coriolis effect. Further, it is apparent that many of the provincial borders, or transition zones, are more effective in reducing dispersal in one

direction than in the other. The Oregonian-Californian Transition Zone, for example, is considerably more effective a barrier to southern animals than it is to northern animals. A large, complex eddy system is present year around just south of Point Conception, influenced by local coastal topography as well as the presence of the northern Channel Islands (Reid et al. 1958; Emery 1960; and others). During the winter the Davidson Current, "trapped" by this eddy system, loses varying amounts of its integrity as it approaches 34°N latitude. North of 34°30'N it "reforms" to continue northward. The much larger California Current does not experience this discontinuity; hence, southward drifting larvae of benthic invertebrates are generally carried well below 34°N latitude. It is for this reason that animals of the Oregonian Province are not uncommonly found on the southern Channel Islands (i.e., Catalina Island, San Nicolas Island, etc.).

The existence of these effects was noted by Hedgpeth (1957) when he remarked, "There is little agreement, for example, on the limits of such provinces on the Pacific coast of North America south of Alaska. . . . this lack of agreement for the limits of provinces in the temperate regions suggests that each worker has used his own criteria." While we are not in full agreement with these statements, it cannot be denied that considerable frustration has arisen out of attempts to delineate zoogeographic provinces in this part of the world. Hedgpeth further remarked that, "At the present state of knowledge, the delineation of provinces, at least in its finer details, is a problem that is not amenable to strict statistical analysis." With regard to the littoral regions of the world's seas, little has occurred in the past 22 years to cause argument with this statement (Valentine's excellent 1966 paper being a notable exception). The few attempts at using strict mathematical techniques to delimit faunal provinces in this environment that we are aware of have not been particularly successful (Parker 1963; Hayden and Dolan 1976). One fruitful product of such attempts has been the discovery of species with very short ranges, or what appear to be narrowly distributed endemics, associated with nodal points shared by the majority of taxa. Newell (1948) suggested that these taxa may in fact represent hybrids and ecotypes associated with the borders of faunal provinces. Although it seems probable that investigations of these narrowly distributed organisms will shed light on some very fundamental issues in animal ecology and biogeography, virtually nothing has yet been accomplished.

One of the most troublesome regions for marine biogeographers is the west coast of Baja California, where the warm temperate region meets the subtropic (the so-called "Sonoran Province" of Dana 1853). This entire 700-mile stretch of coastline harbors numerous bays, lagoons, and esteros that act as refugia for the tropical and subtropical animals from the south, while the exposed rocky coastlines between these lagoons harbor a distinctly temperate-allied fauna. Adding further confusion is the fact that south of the

Mexican border, temperate species tend to be found farther offshore (southern submergence), only to reappear again in the littoral region in localities of upwelling (both Californian and Oregonian species). Dawson (1951) was the first to document this phenomenon in detail. Emerson (1956) presented a map of upwelling areas between the U.S.-Mexican border and 30°N latitude, pointing out that they appear to be at a maximum during spring and summer, the primary reproductive period for most temperate benthic invertebrates, possibly facilitating maintenance of local populations [and] obviating the need for continual larval recruitment from more northerly (or subtidal) habitats.

On the opposite side of the Baja California peninsula, at the same latitudes, cool northern currents are nonexistent and sea water temperatures are largely under the influence of terrestrial climatic conditions of the coastal Sonoran Desert. Garth (1960) realized this in his discussion of brachyuran crab distributions when he stated, "it is also noticeable that when the Gulf of California range of these species is compared with their west coast of Baja California range, the southern limit in the Gulf of California is almost always farther north than on the open Pacific coast."

Garth (1955) originally considered the northern Gulf of California to be part of the warm temperate Californian Province (based on brachyuran crab distributions). Brusca (1979), however, concluded, in agreement with Soule (1960), that the northern Gulf is best considered a subtropical region. This conclusion was based on the examination of distributional ranges of over 1500 shallow water invertebrate species, as well as relevant climatological data.

Unique distributional patterns of shallow water marine invertebrates and plants along the shores of Baja California were discussed by Dawson (1946, 1950, 1951, 1960), Emerson (1952), Soule (1960), Walker (1960), Brusca (1973, 1975, 1979) and Brusca and Thomson (1977). Faunal discontinuities of coastal fishes in the northeastern Pacific have also been associated with temperature aberrations and change (Hubbs 1948; Quast 1968, 1971; and others).

The senior author studied these outer Baja coastal phenomena and tabulated faunal affinities at selected localities. Moving south, the first place in which the number of tropical species exceeds temperate species is Bahía Tortola (so-called Bahía San Bartolome or Turtle Bay, 27°40'N). Based on winter collections of littoral and subtidal (to 20 m) invertebrates in this region, approximately 45% are distinctly tropical and 25% temperate, the remaining 30% being wide ranging or cosmopolitan in distribution (markedly eurythermal species) or unidentified (or undescribed) species. In terms of biomass and abundance, however, temperate forms outweigh the tropical forms. Thus, Bahía Tortola may be considered the northernmost significant refugium for the warm water invertebrate fauna of the Eastern Pacific Zoogeographic Region.

The next sizable lagoon south of Bahía Tortola is Bahía San Ignacio. This bay harbors a large mangrove forest (*Rhizophora mangle, Avicennia germinans* and *Maytenus phyllanthoides*); winter water temperatures here rarely drop below 17°C, the same as in the southern Gulf of California. There is no question as to the dominance of tropical species in this large estuary system both in species richness and numbers of individuals. The next large bay south of this is Bahía Magdalena, a lush semi-tropical system of large lagoons and enormous mangrove forests, harboring very few temperate species of invertebrates. Indeed, few temperate species exist south of Bahía Magdalena at all, even on the exposed headlands. The raw data upon which the foregoing statements are based are available from the authors upon request (also see Dawson 1960; and Brusca 1975 and 1979).

The west coast of Baja California is thus comprised of alternating areas of protected warm waters and exposed colder water regions and forms a discontinuous gradient of the two associated faunas. This makes defining the southern boundary of the Californian Province somewhat arbitrary. The boundary might be established at Bahía de Sebastian Vizcaino (Scammon's Lagoon), which is the northernmost stronghold for a number of warm-water, southern species; or, at Bahía Tortola, which is the first place where there are more tropical than temperate invertebrate species. The mouth of Bahía Tortola also harbors one of the southernmost stands of the temperate giant kelp *Macrocystis* (although Dawson 1960, reported a *Macrocystis* stand at Punta Abreojos, approx. 26.5°N). Several authors have attempted to establish the division at Bahía Magdalena, the southern limit of nearly all temperate shallow water invertebrates, and at Cabo San Lucas where species of the California abalone (*Haliotis*) cease to exist. It seems most logical to accept the region between Punta Eugenio and Bahía Magdalena as a zone of discontinuous overlapping transition between the cool temperate and warm eastern Pacific tropical faunas. Hall (1960) and Valentine (1966), however, designated this short stretch of coastline as a separate province based on molluscan distributions (the Magdalenean Province of Hall; the Surian Province of Valentine). This transition zone appears "banded" on Fig. 2.

Hayden and Dolan's (1976) attempts to define faunal regions based on clustered species range end points agree in part with Valentine (1966), but appear inadequate in certain problematic areas, such as the oceanographically complex coast of western Mexico. This is partly due, no doubt, to choice of animal groups used in the study, and the inappropriate and/or out-of-date literature they relied upon for their distributional data.

Another problematic area is the northern Gulf of California itself. North of the Midriff Islands (Isla Angel de la Guarda and Isla Tiburón) the Gulf experiences strong seasonality in both onshore and offshore water temperatures. The influence of these unstable water temperatures produces a noticeable seasonality in the species composition of the littoral and shallow water marine communities (Brusca 1973, 1979; Brusca and Zimmerman

Ms.; Thomson and Lehner 1976). Onshore water temperatures at Puerto Peñasco (in the northern Gulf of California) may reach 30–32°C in summer, and drop to 10–12°C in winter (Brusca 1979). Naturally, the intertidal region experiences an even greater range of temperatures during periodic exposure to atmospheric conditions. Thomson and Lehner (1976) recorded temperatures as high as 35.5°C, and as low as 4°C in small tidepools at Puerto Peñasco. In addition, the northern Gulf periodically experiences exceptionally cold winters when onshore water temperatures drop to 8–9°C (or less) for several consecutive months. When this happens a massive die-off occurs, particularly among certain macroscopic algae and the stenothermal tropical and subtropical fauna. During these periods, eurythermal and temperate-derived species dominate the littoral habitats. Similar situations have been recorded from Florida (Finch 1917; Storey and Gudger 1936; Miller 1940), the Texas coast (Gunter 1941; Gunter and Hildebrand 1951), and elsewhere. The occurrence of winter mortalities of tropical species in subtropical regions was discussed by Gunter (1957), Kinne (1970), and others. Periodic cold winters and seasonal temperature changes in the northern Gulf of California produce an essentially tropical environment for 9 months of the year, but a warm-temperate environment in the remaining 3 months.

The above discussion has attempted to elucidate the variability in coastal ocean temperatures throughout much of the northeast Pacific. As Hayden and Dolan (1976) pointed out, the covariation of thermal characteristics and distribution of biota is difficult to define. Although the majority of littoral and shallow water marine forms conform fairly well to the zoogeographic provinces presented in Fig. 2, a number which do not may be limited by some factor other than temperature.

2. *The Role of Environmental Temperature in Shallow Water Marine Biogeography.*—The opening sentence in Hedgpeth's (1957) section on *Temperature Bases of Distribution,* "From the outset temperature has been considered the most important single factor governing distribution," was predated 100 years by Dana's (1853) opening sentence, "The temperature of the waters is well known to be one of the most influential causes limiting the distribution of marine species of life," both reflecting long established views that thermal tolerance may limit latitudinal distribution of organisms in shallow marine waters. The concept of temperature being a factor of prime importance in the distribution of marine organisms along the Pacific Coast of North America is so "ingrained" that it is not uncommon to see workers draw inferences regarding ocean temperatures from recorded animal distributions (see Hubbs 1948; Hubbs and Miller 1948). (The relationship between environmental temperatures and thermal tolerance has been tested primarily in the laboratory [Connell 1974], although some workers have taken advantage of the heated effluent from power stations to examine this relationship in the field [review by Naylor 1965]).

There have been a number of excellent review articles published in the last 20 years on the effects of temperature on shallow water marine organisms (Bullock 1955, 1958; Brett 1956, 1959; Gunter 1957; Crisp 1957, 1959, 1964; Precht 1958; Segal 1961; Segal et al. 1963; Lewis 1963; Poljansky 1963; Kinne 1963a, b, 1964, 1970; and others). In pelagic and benthic subtidal marine fauna the thermal death point is usually in the range 30°–35°C (Gunter 1957), but for littoral forms it is considerably higher, around 42°–45°C. Crustaceans from depths of 55 fm cannot withstand high temperatures as well as their congeners from shoal waters (Shelford 1916). Stability of aspartic/glutamic transaminase was higher in mid-intertidal forms (*Mytilus*) than in subtidal species (*Modiolus*), and highest overall in high intertidal species (*Brachiodontes*) (Read 1963, 1967). It has been stated that most temperate and tropical marine animals live very near their thermal maximum, which is also near the optimal temperature level for their metabolic processes (Gunter 1957, Prosser 1973, and others). While it is likely that most shallow water marine animals function best at temperatures nearer their thermal maximum than they do at temperatures dropping much below this maximum, it is obvious from the broad temperature range in which many species exist that only a certain fraction of the gene pool is actually living at these higher, "more optimal" temperatures. Mayer (1914) long ago showed that some Arctic animals may live in water as much as 13°–16°C below their thermal maxima.

All biological processes are regulated, directly or indirectly, by temperature. Hence, as Segal (1961) stated, ". . . we are presented with the improbable situation that arctic poikilotherms metabolize and grow rapidly in icy waters while tropical poikilotherms often metabolize and grow at a more leisurely pace. The explanation, obviously, is that poikilotherms are capable of various compensatory changes in growth rates and metabolic rates in response to changes in environmental temperatures in their habitat." Further, recent work on isozyme chemistry suggests that, within a particular species, genetic variability has produced a multiplicity of enzymes for a specific task, allowing for efficient metabolism through a range of environmental temperatures.

Intertidal and estuarine species have higher thermal tolerances than do subtidal species (Gunter 1957; Hedgpeth 1957; Naylor and Slinn 1958; Southward 1958; Tarzwell 1962; Prosser 1973). Species living high in the littoral region have greater thermal tolerances than those living in the lower zones and shallow subtidal regions (Broekhuysen 1940; Evans 1948; Segal et al. 1953; Bullock 1955; Segal 1956; and others). Todd and Dehnel (1960) showed that heat resistance in the shore crab *Hemigrapsus oregonensis* increases as acclimation to higher environmental temperature increases. Such acclimation experiments have given identical or similar results for a vast array of animal forms, and Menzies and Wilson (1961) showed that pressure change, rather than temperature change, was the cause of death

in shallow water species of crabs and mussels exposed to graduated depths, pressures and temperatures. Within "normal" limits, the absolute temperature seems to have less effect on marine animals than does temperature change (Gunter 1957). Neither optimal nor lethal temperatures are fixed entities, even for a given individual, and most animals can be acclimatized to temperatures far beyond their usual tolerance or exposure. Segal (1961) posed the question, "Can we correlate the ability to acclimate with distribution within a given habitat?" Although only a very small percentage of acclimatization phenomena have been shown to be genetic in nature, Gunter (1957) stated, "Acclimatization in nature is apparently a slow process, resulting in physiological species whose optima and breeding seasons correspond with the prevailing temperature conditions of their respective latitudes." Bullock (1955) concluded that acclimatization of animal species to varying temperature regimes is widespread and of major significance in ecology and evolution. The spawning season of widely distributed organisms corresponds to local temperature conditions. For example: oysters in Long Island Sound may spawn in temperatures as low as 16°C, while southern oysters (of the same species) require 20°C (Gunter 1957); the California goose barnacle, *Pollicipes polymerus,* reproduces at 14°C at sites north of Point Conception, but at temperatures approaching 20°C south of Point Conception (Cimberg 1978). Cimberg (1978) and Loosanoff and Nomejko (1951) considered these phenomena as evidence of physiological races; such conditions are probably common in widely distributed marine species (Gunter 1957).

Valentine's (1966) attempts at a numerical correlation of temperature changes and molluscan faunal changes in the northeast Pacific met with considerable difficulty. He pointed out these difficulties in quantifying the relationship between a species distribution and a single physical factor, such as temperature, and suggested that a combination of factors be used to develop an accurate picture of species distributional phenomena.

The above discussion suggests that in a significant number of taxa the confines of a narrow range of thermal tolerance and its associated geographic limitations are non-existent. Many animals appear to be capable of living in a considerably broader range of thermal conditions than those in which they normally occur. Connell (1974) concluded, "It is difficult to believe that the absolute boundary of most species ranges is determined directly by temperature." Prosser (1973) concluded, "Genetic capacity for temperature acclimation may be greater in animals from environments where temperature fluctuations (annual and diurnal) are considerable, as in temperate zones, than in related animals from areas where the temperature regime is relatively constant (tropics and polar regions)." Indirect proof of this is seen in temperate species that have exceptionally broad latitudinal ranges, or discontinuous (patchy) distributions over many degrees of latitude—the

"outliers" of Forbes and Godwin-Austen (1859). It is in such groups of animals that one might suspect that factors other than temperature are regulating distributional limits. A classic example of this is the American horseshoe crab, *Limulus,* which is common throughout its range from Cape Cod to Florida, and in the Yucatan region of eastern Mexico. *Limulus* is, however, mysteriously absent (or exceedingly rare) on the U.S. Gulf of Mexico coast, and has been reported only twice west of the Mississippi River. The substrates of this coast are adequate, and shore temperatures are well within its normal tolerance range. One widely ranging isopod, *Limnoria tripunctata,* was studied experimentally by Beckman and Menzies (1960). They found this species capable of living through a temperature range of approximately 10°C to 30°C, and reproducing through a range of 15°C to 30°C.

Isopod crustaceans of the genus *Idotea* (family Idoteidae) are, in the northeast Pacific, another enigmatic group, and in the following section we present data which suggest that biological interactions, rather than temperature (or some other physical factor), are controlling the distribution of at least some species in this genus.

Latitudinal Distributions of the Shallow Water Idoteidae of the Northeast Pacific

There are very few species of Idoteidae that are restricted to depths greater than 30 m, although a number of shallow water taxa are known to range occasionally to these depths or undergo submersion in the southern extent of their range. Reference to "shallow water" in this paper refers to depths of less than 30 m. We are not concerned here with species that do not occur above the 30 m isobath, for it is only in water shallower than this that onshore temperature regimes play a direct role.

The distributions of the 31 described species of northeast Pacific shallow water Idoteidae are presented in Figs. 3 to 8, and summarized in Fig. 9.[3] These distributional maps have been generated from the literature as well as the extensive isopod collections at the Allan Hancock Foundation, Scripps Institution of Oceanography and the California Academy of Sciences, and a number of significant range extensions have been incorporated into them.

The genus *Synidotea* contains 15 described species in the northeast Pacific, seven of which occur only in depths greater than 30 m and are not considered in our calculations.[4] The remaining eight species are restricted, with the notable exception of *S. harfordi,* entirely to the cold temperate waters of the Arctic, Aleutian and Oregonian Provinces.

The genus *Saduria* contains 3 described species in the northeast Pacific; all are essentially Arctic in distribution, although *S. enotomon* is known to occur as far south as central California where it is found only at considerable depths (i.e., southern submergence phenomenon).

The genus *Edotea* contains only a single described species in this region,

FIG. 3. DISTRIBUTION OF SHALLOW
WATER SYNIDOTEA SPECIES IN THE
NORTHEAST PACIFIC.

1. S. bicuspida
2. S. nebulosa
3. S. nodulosa
4. S. ritteri
5. S. pettiboneae
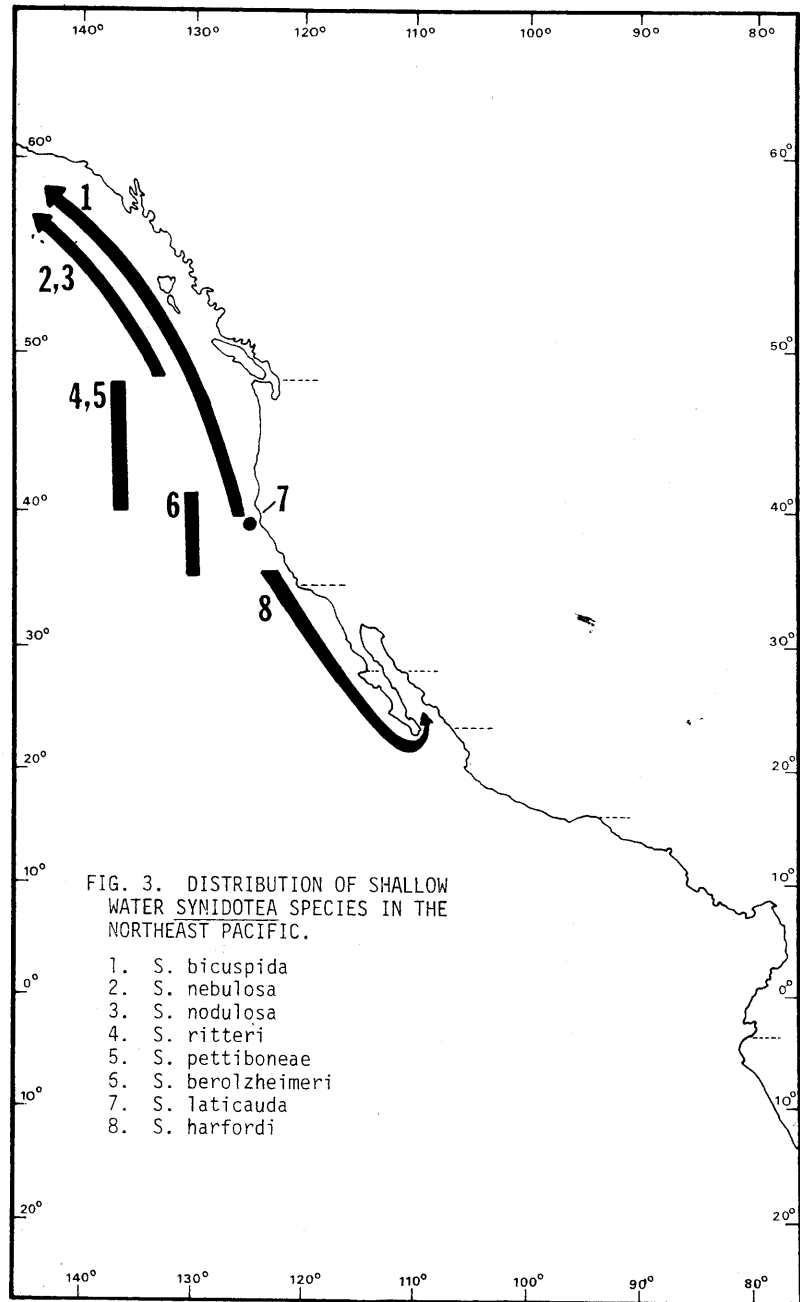6. S. berolzheimeri
7. S. laticauda
8. S. harfordi

Fig. 3.   Distribution of shallow water species of *Synidotea* in the northeast Pacific. (Dashed lines along coast represent provincial boundaries.)
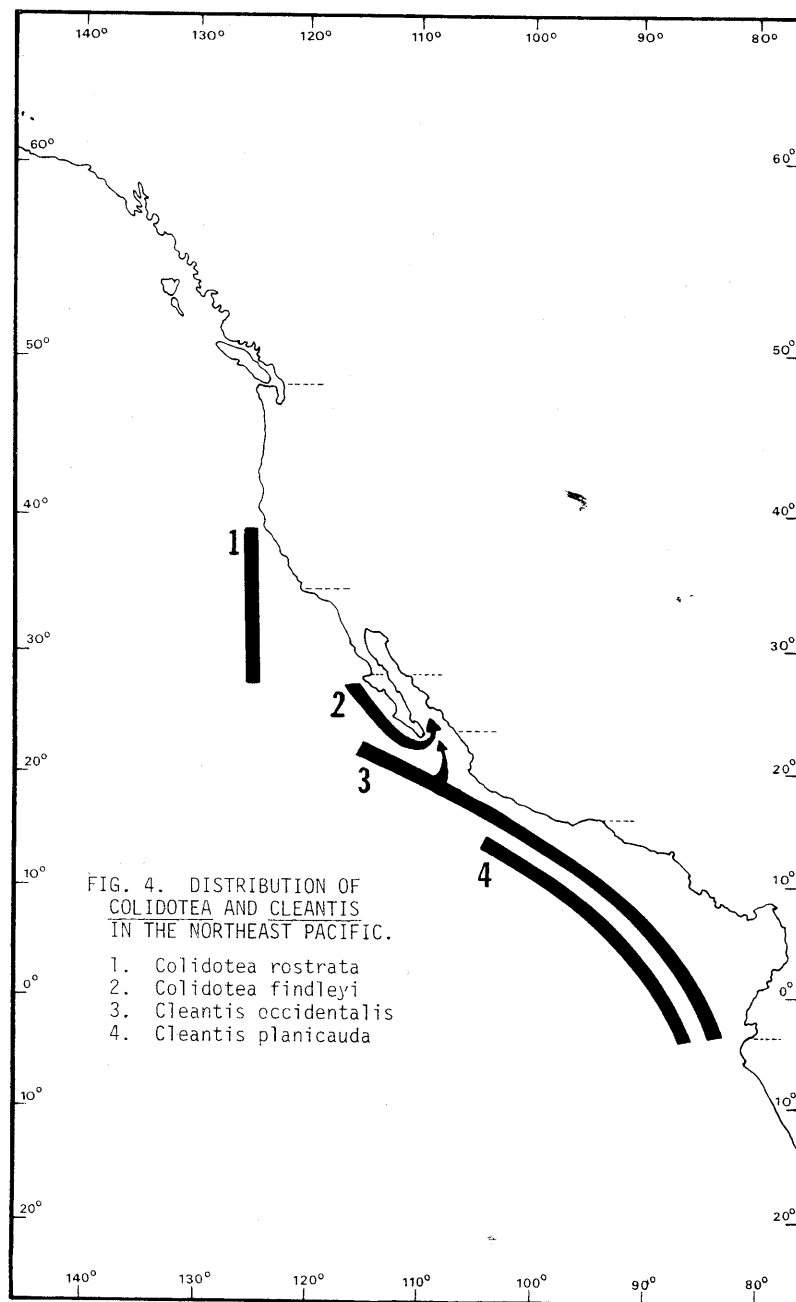
FIG. 4. DISTRIBUTION OF
COLIDOTEA AND CLEANTIS
IN THE NORTHEAST PACIFIC.

1. Colidotea rostrata
2. Colidotea findleyi
3. Cleantis occidentalis
4. Cleantis planicauda

Fig. 4. Distribution of species of *Colidotea* and *Cleantis* in the northeast Pacific. (Dashed lines along coast represent provincial boundaries.)
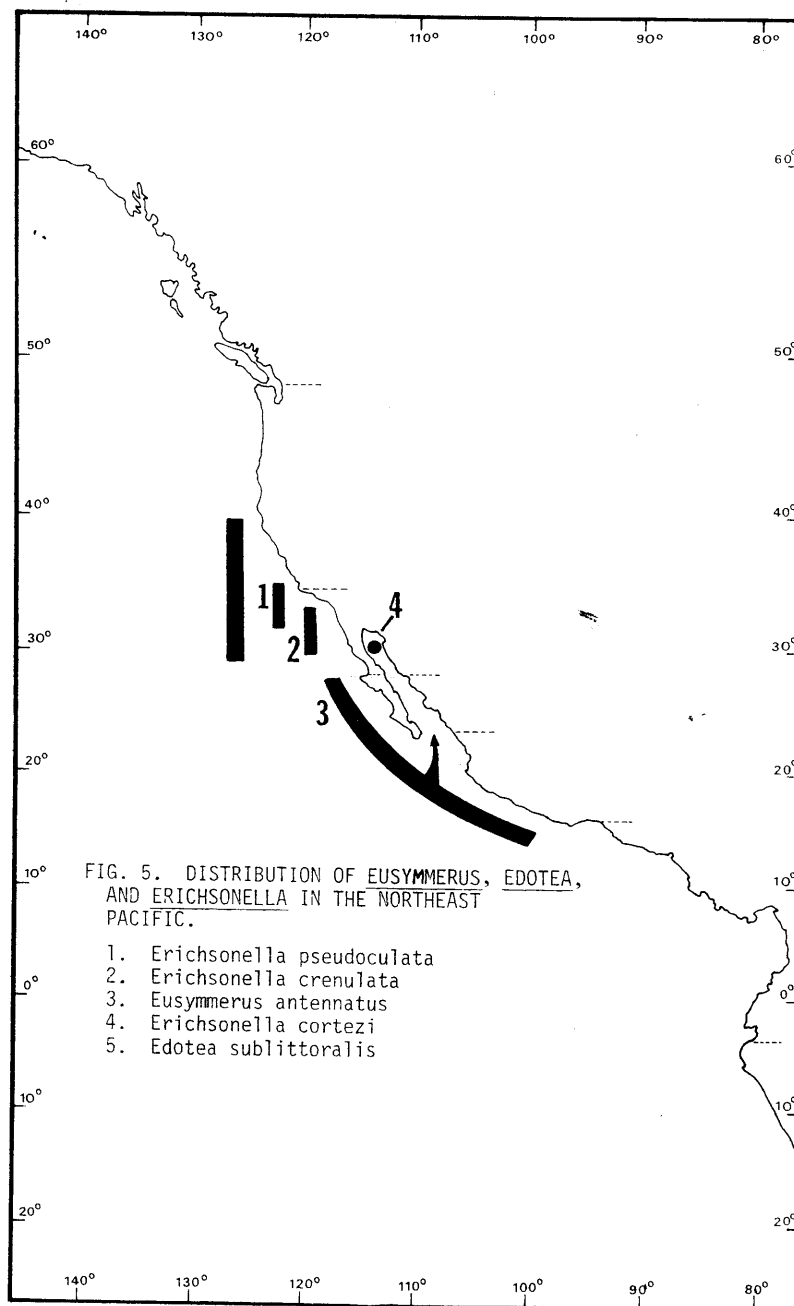
FIG. 5. DISTRIBUTION OF EUSYMMERUS, EDOTEA,
AND ERICHSONELLA IN THE NORTHEAST
PACIFIC.

1. Erichsonella pseudoculata
2. Erichsonella crenulata
3. Eusymmerus antennatus
4. Erichsonella cortezi
5. Edotea sublittoralis

Fig. 5. Distribution of species of *Erichsonella* and *Eusymmerus* in the northeast Pacific. (Dashed lines along coast represent provincial boundaries.)
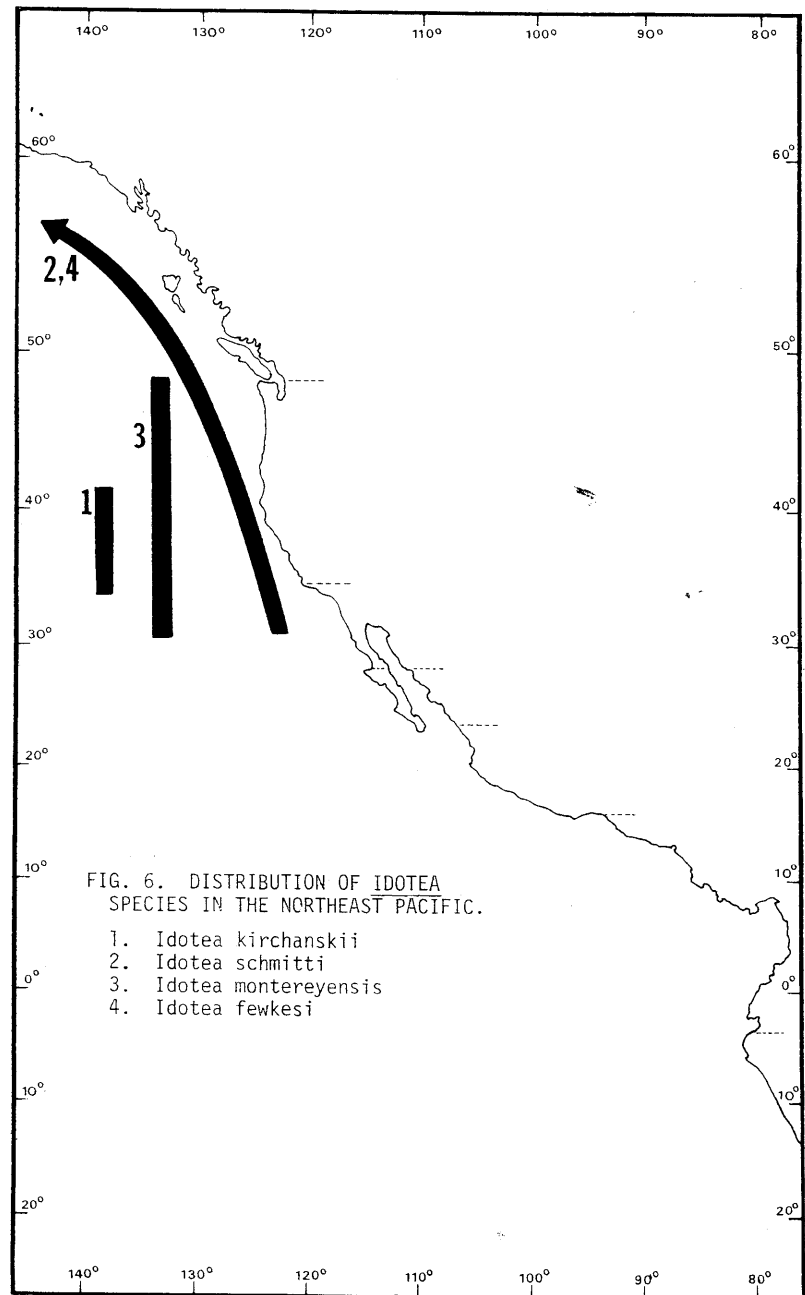
Fig. 6. Distribution of species of *Idotea* in the northeast Pacific. (Dashed lines along coast
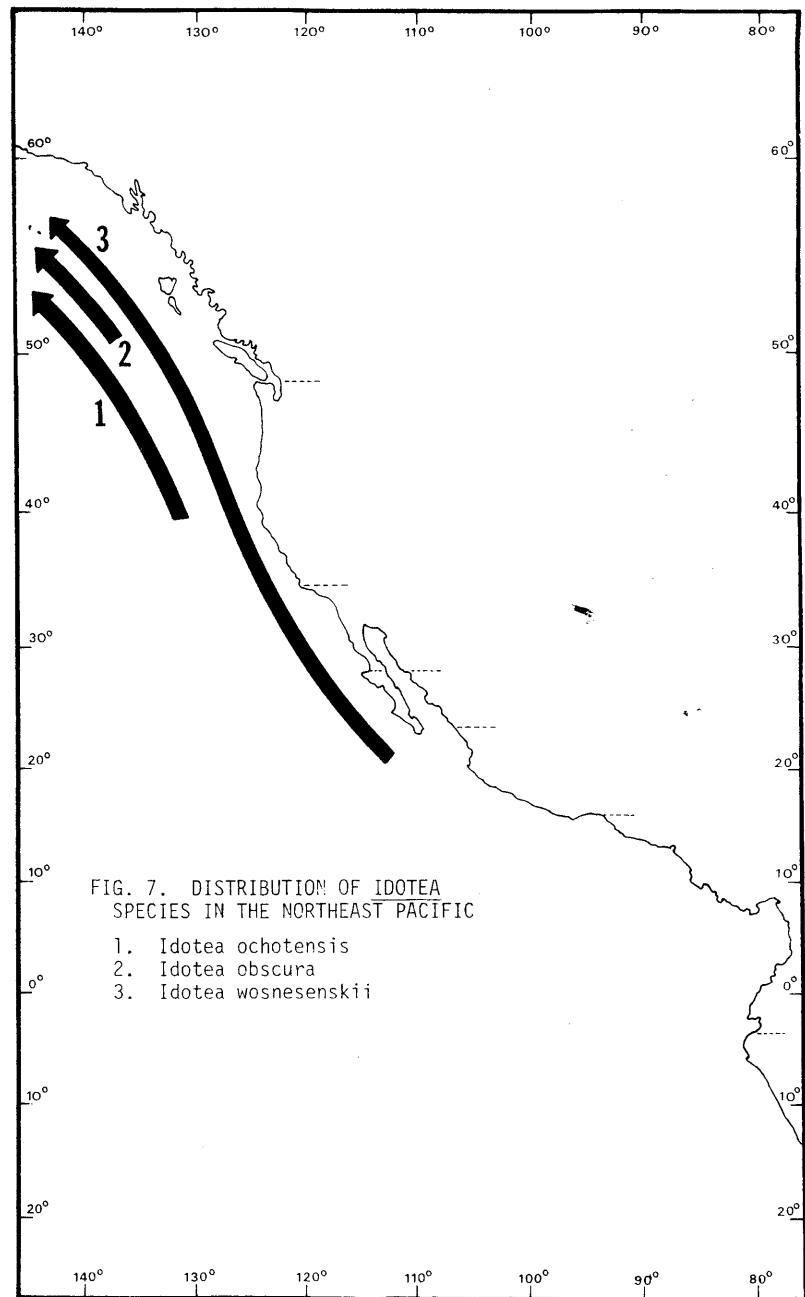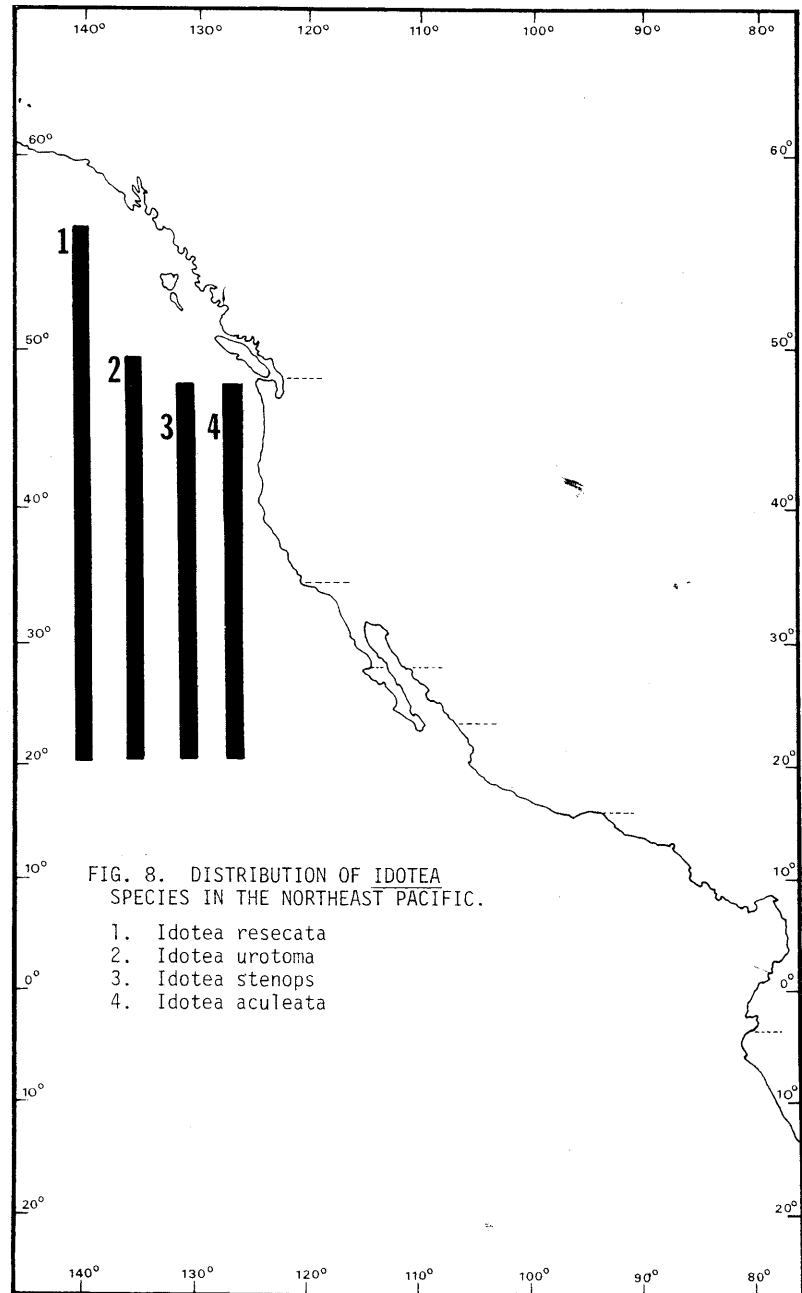represent provincial boundaries.)

FIG. 7. DISTRIBUTION OF IDOTEA
SPECIES IN THE NORTHEAST PACIFIC

1. Idotea ochotensis
2. Idotea obscura
3. Idotea wosnesenskii

Fig. 7.   Distribution of species of *Idotea* in the northeast Pacific. (Dashed lines along coast represent provincial boundaries.)

FIG. 8.   DISTRIBUTION OF IDOTEA
SPECIES IN THE NORTHEAST PACIFIC.

1.   Idotea resecata
2.   Idotea urotoma
3.   Idotea stenops
4.   Idotea aculeata

Fig. 8.   Distribution of species of *Idotea* in the northeast Pacific. (Dashed lines along coast represent provincial boundaries.)

Table 1. Summary of provincial distributions of northeast Pacific shallow water Idoteidae. *Idotea* = 2.64 zoogeographic ranges, non-*Idotea* = 1.84 zoogeographic ranges. Dotted lines indicate occasional occurrences.

Species	Distribution (by province)						
	Arctic	Aleutian	Oregonian	Californian	Cortez	Mexican	Panamic
Saduria entomon	---	---	---				
sabini	---						
sibirica	---						
Synidotea biscuspida	---	---	········				
nebulosa	---	---	········				
nodulosa	---	---					
harfordi			---	---	········		
berolzheimeri			---	---			
laticauda			---	---			
pettiboneae			---				
ritteri			---	---			
Edotea sublittoralis			---	---			
Colidotea rostrata			········	---			
findleyi				········	---		
Erichsonella crenulata				---	---		
pseudoculata				········			
cortezi					---		
Eusymmerus antennatus				········	---		
Cleantis occidentalis					---	---	---
palnicauda						---	---

Table 1. Continued.

Species	Distribution (by province)						
	Arctic	Aleutian	Oregonian	Californian	Cortez	Mexican	Panamic
Idotea obscura	-----	-----					
ochotensis	-----	-----					
wosnesenskii		-----	--------	-------	....		
fewkesi		-----	--------	-------	....		
*resecata**			--------	-------	....		
aculeata			--------	-------			
kirchanskii			--------	-------			
montereyensis			--------	-------			
urotoma			--------	-------	....		
stenops			--------	-------	....		
schmitti			--------	-------			

* Examination of a large series of *Idotea rufescens* Fee 1926 has shown it to possess a maxillipedal palp of either 4 or 5 articles, hence making necessary its removal to the subgenus *Pentidotea*. In addition, we have found most of the characters used by Menzies (1950) to distinguish this species from *I. resecata* to be unreliable. We presently consider *I. rufescens* to be a *species inquirenda*, whose range is essentially identical to that of *I. resecata*.

E. sublittoralis, known from the temperate Oregonian and Californian Provinces. The genus *Cleantis* was previously thought to be represented in western North America only by *C. occidentalis,* a tropical form ranging from the Gulf of California (Cortez Province) south to Ecuador (Panamic Province). We now have specimens of *C. planicauda* from southwest Mexico, establishing it as an amphiamerican form. The genus *Eusymmerus* contains a single described species, *E. antennatus,* which has its principal range in the Cortez and Mexican Provinces, although occasional records from the southern extent of the Californian Province exist.

Erichsonella contains three described species in the east Pacific; two are Californian and one is restricted to the Cortez Province. The genus *Colidotea* consists of three described species. A reasonable argument could be made that this genus is subtropical in origin, for its distribution is as follows; *C. rostrata,* restricted largely to the Californian Province although occasional records from the Oregonian Province exist; *C. findleyi,* restricted largely to the Cortez Province although occasional records from the Californian Province exist; and, *C. edmondsoni,* known only from Hawaii.

The final idoteid genus, *Idotea,* has 11 valid, described species occurring in the northeast Pacific. The status of these species is reasonably stable although a few new species are expected to be described in the near future.[5] *Idotea* is the most broadly ranging genus of the family in this region, spanning five zoogeographic provinces (Arctic, Aleutian, Oregonian, Californian and Cortez). Several species range through four of these provinces, the most widely ranging being *I. fewkesi, I. resecata,* and *I. wosnesenskii.*

It is apparent from these data (and the work of others, for example: Menzies, 1950; Menzies and Miller, 1972; Kussakin, 1973; and Brusca and Wallerstein, 1977) that the family is centered in cool water.[6] It is within the Oregonian and Californian Provinces (in the northeast Pacific) that the greatest number of shallow water idoteid species may be found (20 and 16, respectively). However, it is also apparent that a number of warm water genera have also evolved in this general region (*Colidotea, Eusymmerus, Erichsonella*). Further, certain species of the genus *Idotea* maintain populations through a broad latitudinal range, often extending through three or four zoogeographic provinces and into the warm southern waters of the Cortez Province (i.e., *Idotea urotoma, I. aculeata, I. resecata, I. stenops,* and *I. wosnesenskii*). In some cases these southern records can be associated with regions of cool water upwelling, but many cannot. The sporadic occurrence of these species outside their principal ranges, in such warm coastal localities as Punta San Telmo and Bahía La Paz (in the Gulf of California), suggests that certain members of this genus are considerably more eurythermal than previously thought. The mean range of the shallow water *Idotea* species in the northeast Pacific traverses 2.64 zoogeographic provinces (3.2 if Valentine's Surian Province is recognized). By comparison,

the mean shallow water species range for all other genera of Idoteidae (in the northeast Pacific) traverses only 1.85 zoogeographic provinces.

Upon examination of the data associated with the southern records of these widely ranging species of *Idotea,* we began to suspect that biological factors might be playing a more significant role in regulating their southern distributional limits than physical factors. The basis for this suspicion was two-fold. First, these species of *Idotea* are quite rare south of Punta Eugenio (on the west coast of Baja California), which is a major geographic break between much of the cool Californian fauna and the warmer Mexican/Cortez faunas. However, when found, they have usually been collected in moderately large numbers which often include gravid females. This rules out the possibility that all southern records are accidental occurrences of individuals that have floated south on algae drifting in the California Current system. Our second clue was that, in every case, collections from the southern localities containing specimens of *Idotea,* possess ONLY *Idotea,* and none of their confamilial warm-water genera or species (i.e., *Colidotea, Eusymmerus, Erichsonella* and *Cleantis*).

One of the best examples of eurythermy in the genus *Idotea* is the case of *I. urotoma.* We have examined over 500 specimens of this species from San Juan Island, Washington, to La Paz, in the Gulf of California. Mean monthly sea surface temperatures in the vicinity of San Juan Island are 8.5°C to 13.5°C (Churgin and Halminski 1974 and Johnson 1961). September sea surface temperatures at La Paz are about 30°C (from Robinson 1973, and the senior author's field data). This is a thermal range of at least 21 centigrade degrees for this species. Although its occurrence south of Punta Eugenio is rare, our records indicate that reproducing populations occasionally become established along the warm shores of southern Baja California. Data from our samples record this species in water temperatures ranging from 13.9°C (near Ensenada) to 24.2°C (in Bahía La Paz). The single La Paz collection, taken on an overcast afternoon in early November, included males, females and ovigerous females. This record apparently represents a sample of a population that had survived the warm summer water temperatures of the La Paz region (29°–31°C). Even if one were to postulate that the entire La Paz population had rafted into the Gulf from the outer coast of the peninsula, it would still have experienced similar warm temperatures during its journey south of Bahía Magdalena and around Cabo San Lucas. A similar situation exists for *I. aculeata.*

These data suggest that *I. urotoma* is capable of existing in waters much warmer than those of the Californian Province, and hence some factor other than temperature is restricting their southern distribution. It is our contention that, in at least some species of *Idotea,* the southern distributional limit may be regulated by biological interactions. There are three types of biotic factors that may be responsible for the inability of species such as *I. rese-*

cata, *I. aculeata,* and *I. urotoma* to extend their range permanently south of Punta Eugenio: competition, predation, and lack of suitable substrate.

Competition would most likely occur with the very similar idoteid isopods *Colidotea findleyi, Erichsonella cortezi,* and/or *Eusymmerus antennatus.* These species prefer brown algae of the genus *Sargassum* as both a substrate and food source, and hence could be responsible for excluding species of *Idotea* from these subtropical phaeophytes. The importance of competition in regulating the distributions of tropical marine life has been amply demonstrated (see Briggs 1967; Thorson Ms.; Sheltema 1969; Bakus 1969; and others). Rees (1975) has shown that competitive interactions and substratum preferences exist between two species of intertidal sphaeromatid isopods, *Gnorimosphaeroma oregonensis oregonensis* and *Exosphaeroma amplicauda.* Equally likely is the possibility that the presence of greater numbers (and a greater variety of species) of predaceous grazing fishes and invertebrates are responsible for restricting *Idotea* from the west American subtropics. It is well known that fishes are the primary predators of members of this genus (see Rauschenplatt 1901; Richardson 1905; Popiel 1951; and Carausu 1955). Hobson (1968) found that, of 46 species of predatory fishes he studied in the Gulf of California, only six did not rely on crustaceans for some part of their diet. Thomson and Lehner (1976, and pers. comm.) found that the 25 most common intertidal fishes of the northern Gulf of California specialized on a diet of benthic crustaceans. Clearly, both competition and predation may be working simultaneously to exclude *Idotea* from this region. Most eastern Pacific *Idotea* show a strong preference for the large brown algae of the order Laminariales which they utilize not only as living space but as a food source (Jones 1971; Brusca and Wallerstein 1977; and pers. observations).

The Phaeophyta may have evolved in the temperate latitudes, to have only recently invaded the tropics (Bakus 1969). Judging by the paucity of idoteid species in these lower latitudes and their concentration in the temperate regions, one could reason the same sort of recent invasion of warm water habitats by this family of valviferan isopods. Indeed, both the idoteids and the brown algae reach their greatest abundance in the northeast Pacific, in the mid and southern temperate latitudes (the Oregonian and Californian Zoogeographic Provinces). Bearing this in mind, and considering the intimate association of the majority of idoteid species with brown algae, it is not unreasonable to speculate that the Phaeophyta and the idoteids have undergone some degree of coevolution.

Many *Idotea* have also been shown to be capable of altering their feeding habits when necessary, even switching to a scavenging mode upon occasion (Naylor 1955a; Sywula 1964). On the California coast they are most commonly found on species of *Macrocystis, Nereocystis,* and *Egregia,* and north of San Francisco on *Fucus, Pelvetiopsis* and *Porphyra,* although *I.*

urotoma is also common of surfgrass (*Phyllospadix*) and under rocks in the mid- and low intertidal regions. All species of large laminarians cease to exist just south of Punta Eugenio (around Bahía Tortola or Turtle Bay).[7] Perhaps *I. urotoma* and *I. resecata* cannot successfully compete or avoid predation, living upon a small tropical alga such as *Sargassum*, particularly if it is already inhabited by the warm water idoteids *C. findleyi*, *Eusymmerus antennatus* and *Erichsonella cortezi*. Both *I. resecata* and *I. urotoma* are large species, adults reaching 55 mm and 26 mm in length, respectively. This large size might afford predaceous fishes with an easy meal in comparison to the much smaller species of *Colidotea*, *Eusymmerus*, and *Erichsonella*, which reach lengths of 22 mm, 12 mm, and 15 mm, respectively.

The determination of what factors may regulate the southern distribution of these eurythermal species of *Idotea* is the subject of the junior author's continuing research. One of the first studies to be performed will be a series of thermal acclimation and critical thermal maximum experiments, in which individuals from a large range of latitudes will be tested. These experiments will test the null hypothesis that temperature is not limiting the southern distribution of certain species of *Idotea*. They will also assess the possible existence of latitudinal gradients in thermal tolerance and establish the actual *in vitro* upper thermal limits of the species in question. Based upon the abundant literature on this subject for non-isopod crustaceans and other shallow water invertebrates, the presence of such a latitudinal or "clinal" gradient in thermal tolerance is predicted.

As a preliminary assessment of the physiological capabilities of one wide ranging species, *Idotea urotoma*, we attempted to acclimate a population of 150 individuals from Catalina Island (California) to temperatures considerably above the normal range of water temperatures for that locality. The results of these experiments are presented below.

Experimental Data

1. Methods and Materials.—One hundred and fifty *Idotea urotoma* were placed in 15 one-gallon jars, the jars in turn being situated in a large water bath (24 × 60 × 180 cm). Only adults were used, but both males and females (some ovigerous) were included in each jar. Each jar contained, in addition to 10 isopods, a small clump of cleaned surfgrass (*Phyllospadix scouleri*) which served as both food and substrate. Each jar was aerated and monitored regularly for temperature and dissolved oxygen content (using a Y.S.I. model 57 oxygen-temperature meter with submersible probe). The water bath was provided with two 30 cm, 200 watt, thermostatically controlled, submersible heaters (Jager brand, accurate to ±1°C). Air curtains were used in the water bath to assure water circulation and even heating. As a control, an identical culture was maintained in a water bath adjacent to the experimental arrangement. The control was not heated, but kept at
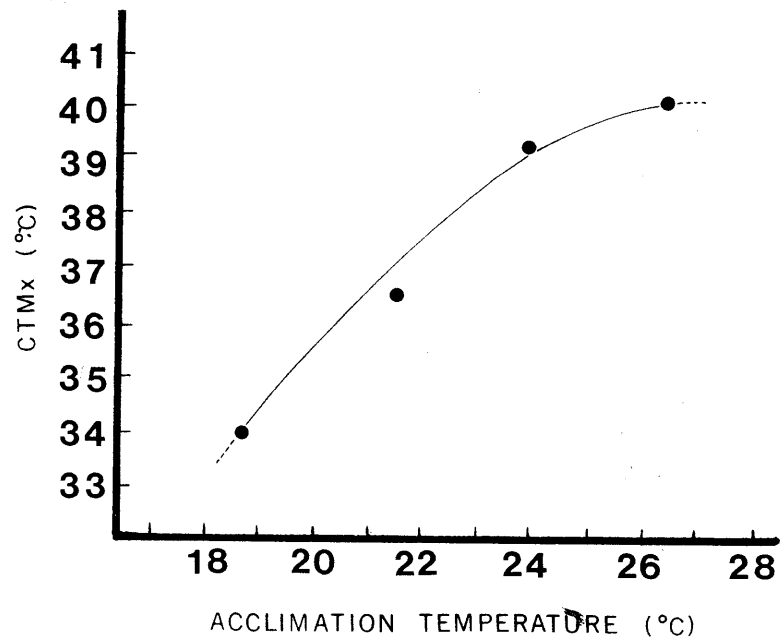
Fig. 9. Summary of experimental data on *Idotea urotoma*—acclimation temperature vs. critical thermal maximum.

ambient temperatures by use of the laboratory's circulating sea water system.

The temperature of the water bath was raised slowly, from ambient, at a rate of approximately 0.7°C/day. Based upon previous studies, this rate was judged to be sufficiently slow to allow acclimation to occur. Every three days the animals of one jar were removed and subjected to a standard critical thermal maximum (CTMx) test. This procedure continued until death of the culture occurred.

The CTMx test consisted of placing the animals in a 250 ml beaker, this in turn being placed in a water bath and heated rapidly until 90% of the isopods were dead (LD-90). Preliminary testing revealed that the death point was observable by cessation of pleopod beat and antennal twitch, revival being impossible beyond this point. During the CTMx experiments the water was aerated and monitored continuously for temperature and dissolved oxygen content, to assure that the animals suffered no oxygen stress. Dissolved oxygen levels during CTMx experiments ranged from 6 to 9 ppm. Bulnheim (1974) showed that thermal acclimation has no significant effect on the rate-temperature relations of respiratory metabolism (in *Idotea balthica*).

2. Results and Discussion.—Over a period of 13 days we were able to acclimate *I. urotoma* to a maximum of 28°C. No latent period of acclimation

Table 2. Summary of experimental data on *Idotea urotoma*—critical thermal maxima (CTMx).

Experiment number	Acclimation temperature	Acclimation time (days)	Temperature at 90% death (CTMx)
1	18.8°C (ambient)	2	34°C
2	21.5°C	7	36.5°C
3	24°C	11	39.3°C
4	27°C	13	40°C

was observed. This is in contrast to lobster (*Homarus americanus*) which has a latent period of 10 days (McLeese 1956), but similar to bullhead (Brett 1944), large mouth bass (Hathaway 1927) and a marine goby, *Gillichthys mirabilis* (Sumner and Doudoroff 1938). At an acclimation temperature of 27°C the CTMx was 40°C. The mean annual range of onshore temperatures at Catalina Island is 12.9°C to 20.9°C,[8] while the ambient temperature at which the isopods were collected for this experiment was 18.5°C. These data are presented in Fig. 9 and Table 2.

It is apparent from this brief, preliminary study that *I. urotoma* (of a Catalina Island genotype) are capable of living at temperatures considerably above those to which they are normally subjected. Offshore sea surface temperatures at the southern extent of this isopod's principal range, Punta Eugenio (Baja California), attain an annual maximum of about 21°C (Robinson 1973) in October, and onshore temperatures probably range several degrees above this. The maximum acclimation temperature of the Catalina individuals tested was still 5 to 8 centigrade degrees in excess of the warmest yearly mean that the species experiences within its principal range.

Assuming even the slightest increase in ability to acclimate to warmer environmental temperatures, it would not be unreasonable to expect individuals of a genotype from Baja California to acclimate to 30° or more. These data are consistent with those of others (see part two of Introduction) working with other invertebrate taxa. They are also in agreement with Naylor (1955b) who recorded lethal temperatures of 33°-35°C for four species of European *Idotea*, including *I. granulosa* and *I. chelipes*, and Furch (1972) who showed a positive correlation between degree of heat resistance and acclimation temperature in *I. balthica*. These findings also echo those of Sywula (1964) who concluded that *I. chelipes*, *I. balthica* and *I. granulosa* should be considered eurythermal species.

During the two week period of acclimation (from 18.5°C to 28°C) a number of nonovigerous females became gravid, and a number of previously ovigerous females released manca, which also survived, in apparent good health, for the duration of the experiment. Numerous individuals also molted normally.

Summary

1. General oceanic circulatory patterns for the northeast Pacific coast are reviewed, and the hydrological complexity of this region discussed. Much of this coast, particularly between Oregon and northwestern Mexico, experiences considerable variation (monthly and yearly, as well as long-term cycles) in water temperature.

2. Pertinent literature on temperature as a factor controlling the distribution of shallow water benthic invertebrates is reviewed. Numerous examples illustrate that eurythermy, long-term temperature acclimation, and various types of compensatory metabolic changes occur in a variety of invertebrate taxa, often demonstrating the ability of a species to live in thermal regimes well beyond those occurring in its actual geographic range.[9]

3. Distribution of NE Pacific species of the family Idoteidae is reviewed. The family is seen to be centered in cool to cold water; however, in the northeast Pacific several genera penetrate significantly into the warm subtropical waters of western Mexico. The genera *Synidotea* and *Saduria* are restricted entirely to the Arctic, Aleutian and Oregonian Provinces, with the notable exception of *Synidotea harfordi*; *Edotea* occurs in the cold and warm temperate (Oregonian and Californian) provinces; *Erichsonella* and *Colidotea* occur in the Californian-Cortez Provinces; *Cleantis* and *Eusymmerus* are strictly tropical/subtropical in distribution; and *Idotea* ranges broadly through five provinces (Arctic, Aleutian, Oregonian, Californian and Cortez).

4. Although isolated occurrences of certain species of *Idotea* have been recorded from south of their principal range (south of Punta Eugenio, Baja California), they are apparently not capable of establishing significant populations in these warmer waters.

5. In experimental studies, a southern California (Catalina Island) population of *Idotea urotoma* was acclimated to 28°C. This is 9.5°C above ambient for that time of the year (March 1978), and 7.9°C above the mean annual maximum for the Catalina habitat. At ambient temperature the critical thermal maximum (CTMx) for this population was 34°C. At an acclimation temperature of 27°C their CTMx was 40°C.

6. The thermal tolerances of these wide ranging species of *Idotea* are such that temperature might be ruled out as the primary factor governing their southern limits.

7. Species of the genera *Idotea, Colidotea, Erichsonella* and *Eusymmerus* show a strong preference for living upon brown algae (Phaeophyta), which they utilize as both a substrate and a food source. The southern limit of *Idotea* coincides with that of these preferred algae and also with the northernmost occurrence of the warm-water idoteid genera *Colidotea, Erichsonella* and *Eusymmerus*. The latitudes at which this ecological replacement

takes place coincide with the California-Cortez Transition Zone. It is a region of considerable increase in species diversity.

8. We hypothesize that the southern distributional limit of at least some species of northeast Pacific *Idotea* is regulated primarily by biotic, rather than abiotic factors.

Acknowledgments

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Footnotes

[1] The existence of a warm temperate zone in the northeast Pacific appears to have been first documented by Dana (1853), subsequently disregarded, and then again reestablished by Garth (1955). The latter author was able to show that Ekman (1935, 1953) lacked sufficient data to recognize a warm temperate fauna on this coast.

[2] Workers are cautioned that in many works predating Briggs (1974) the term Panamic Province is considered synonymous with the Eastern Pacific Zoogeographic Region. In addition, Briggs considered the Gulf of California to be a disjunct warm temperate province, rather than a subtropical region. Judging by the relative numbers of fish and invertebrate species, there appears to be no question that this region should be considered subtropical in nature.

[3] The taxonomy used in this report is based upon Menzies (1950), Kussakin (1955), Menzies and Miller (1972), Rafi (1972), and Brusca and Wallerstein (1977).

[4] *Synidotea spinosa anadyrensis, S. acuta, S. pallida, S. erosa, S. angulata, S. calcarea,* and *S. magnifica.*

[5] The genus *Idotea* is presently being revised by F. Rafi (National Museum of Canada).

[6] Kuşsakin (1973) calculated that 126 species, or about 77% of the described species of Idoteidae occurred in cold and cold-temperate waters. Although he did not separate his data by genus, it is apparent from his figures that 36% of the species of Idoteidae he considered were wide ranging, occurring in both shallow warm seas and shallow cold seas. We suspect most of these were members of the genus *Idotea.*

[7] Although it is difficult to find published statements that document the absence of the Laminariales in the tropics (Bakus 1969), anyone who has worked in the lower latitudes is aware of the paucity of phaeophytes in this region. Perhaps this fact has been too obvious to publish. Temperate latitudes harbor a higher diversity of benthic algae than the tropic and arctic regions (Bakus 1969).

[8] Temperature data provided by Dr. R. Cimberg, based on pier data for 1972–1975 (see Cimberg 1978).

[9] We have not dealt in this study with temperature related phenomena below the organismal level, although studies of temperature adaptations at the cellular and subcellular levels abound.