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## Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae)

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**ABSTRACT.** Behavioural, morphological and distributional patterns of idoteid isopods (family Idoteidae) from the northeast Pacific are analysed with respect to the hypothesis of increasing predation pressure from fishes in the lower latitudes. Minimum reproductive size and maximum body length of idoteids both decrease with decreasing latitudes; body ornamentation increases with decreasing latitudes. Members of the tropical and subtropical genera *Parasymmerus*, *Eusymmerus*, *Colidotea* and *Erichsonella* are smaller and more ornamented than species of the temperate genus *Idotea*. The subtropical isopod *Colidotea findleyi* is a 'swimmer', whereas the larger, more conspicuous, temperate species *Idotea urotoma* shows no preference between 'swimming' and 'nonswimming' behaviour. In laboratory predation experiments, the tropical wrasse *Thalassoma lucasanum* selected larger isopod prey items, as well as preferring *Idotea urotoma* over *Colidotea findleyi* of equal length.

The geological evolution of the region is discussed in regards to vicariant events, shifting faunal waves, and modern zoogeographic patterns of idoteid isopods. Data obtained in this study support the hypothesis that fish predation may play a major role in controlling the southern range limits of temperate rocky-shore isopods, and that this same pressure may have affected the evolution of idoteid isopod body size and morphology in the northeast Pacific.

### Introduction

Brusca & Wallerstein (1979b) recently examined the zoogeography of the isopod family Idoteidae in the northeast Pacific, questioning the absolute role of temperature in determining species distributions, and suggesting that the southern range limits of some species may be strongly influenced by biotic factors. Similar conclusions regarding latitudinal ranges of marine species have been reached by Newman (1960), Naylor (1965), Connell (1974), Nelson (1979a, 1980a), Lubchenco (1980) and others. The two major questions addressed in the present study are: (1) what factors are regulating the southern geographic range limits of the rocky shore idoteid isopods

that occasionally or principally inhabit the subtropical Gulf of California region; and (2) what morphological characteristics are likely to be evolutionarily derived products of these regulatory factors.

Macrocrustaceans have long been known as an important and abundant food source for marine and freshwater fishes (Hrbáček, 1962; Hardy, 1965; Randall, 1967; Schmitt, 1971; Heck, 1979). In rocky intertidal and subtidal habitats peracarid crustaceans, especially amphipods and isopods, are dominant food items for many fish species (e.g. Hobson, 1965, 1968, 1974; Quast, 1968; Hobson & Chess, 1976; Vermeij, 1978; Christensen, 1978; Zander, 1979). A number of recent authors have discussed the importance of

predation to crustacean evolution, community structure and population dynamics (e.g. Newman, 1960; Cooper, 1965; Strong, 1972; Vince, Valiela & Backus, 1976; Heck & Wetstone, 1977; Kettle & O'Brien, 1978; Nelson, 1978, 1979a, b, 1980a, b; O'Brien & Vinyard, 1978; Caine, 1979; Heck, 1979; O'Brien, Kettle & Riessen, 1979; Stoner, 1979). Vertical migration of demersal zooplankton (Hobson & Chess, 1976; Robertson & Howard, 1978), duration of amplexus (Strong, 1973), and colour polymorphism (Moreira, 1974; Salemaa, 1978, 1979a; Hairston, 1979) are just a few examples of how fish predation is believed to have affected the evolutionary paths of crustaceans.

Shallow water idoteids are common inhabitants of rocky shores. Some species show a preference for specific habitats, such as a particular plant or a mussel bed community (Menziés, 1950; Jones, 1971; Lee & Gilchrist, 1972). Nearly all are cryptic and match the colour of their substrate with amazing precision (Lee, 1966a, b, 1972; Salemaa, 1978, 1979a). Most are omnivores with a tendency toward herbivory, occasionally feeding on dead and decaying animal material (Kjennerud, 1950; Naylor, 1955a; Nicotri, 1980). Accounts of their general ecology can be found in Howes (1939), Naylor (1955b), Sywula (1964), Muus (1967), Jansson & Matthiesen (1971), Salemaa (1979b) and Strong & Daborn (1979a, b).

In order to determine if fish predation could be playing a role in regulating the southern distribution of temperate, rocky shore idoteid isopods, a series of prey choice experiments was conducted using a known tropical fish predator of Crustacea. Previous studies suggested that size selective predation of larger prey individuals should occur, but that body pigmentation, behaviour, prey density, prey distribution, habitat (algae) cover, and predator size could all act as modifying factors (e.g. Brooks & Dodson, 1965; Strong, 1972; Dodson, 1974; Eggers, 1977; Murdoch, 1979; O'Brien, 1979; Stoner, 1979). Presented below are: (1) the results of our laboratory predation experiments; (2) new morphometric data regarding latitudinal trends in the Idoteidae; and (3) data from a comparative behavioural study between a subtropical and temperate species in the isopod family Idoteidae.

## Methods

Females and primary males of the eastern tropical Pacific wrasse *Thalassoma lucasanum* Gill, a known crustacean predator (Hobson, 1968; Thomson *et al.*, 1979), were used for the predation experiments. Specimens of the temperate isopod species *Idotea urotoma* Stimpson were collected locally from a large year-round population at Point Fermin, San Pedro, California (33° 42' N 118° 17' W). Subtropical isopods (*Colidotea findleyi* Brusca and Wallerstein) were collected from the northern Gulf of California, Mexico (c. 31° N, 114° 30' W).

Animals were maintained previous to and during each experiment in 79-litre aquaria (60 × 50 × 25 cm) with filtered sea water (35‰). Each aquarium was maintained within a temperature range of 22.5–24.5°C by a Jäger brand submersible heater. Overhead fluorescent lights provided uniform illumination during ambient daylight hours.

Data were tested for significance ( $P = 0.05$ ) by the binomial test for one sample data and by a chi-square test for two sample cases (Siegel, 1956).

## Behaviour

The following experiment was performed in order to determine if behavioural differences in swimming exist between *Idotea urotoma* and *Colidotea findleyi*. In each trial an isopod was placed alone in a 10 cm petri dish containing filtered seawater, and allowed to remain undisturbed for a 1 min acclimating period. The dish was then lowered to the surface of the aquarium, gently submerged, and the isopod poured out. The locomotory behaviour of each individual was classified as either 'swimmer' or 'nonswimmer'. For the purposes of this study 'swimmer' refers to those individuals that control their movement by the use of pleopod and antennal beating, whereas 'nonswimmer' refers to individuals that passively drift downward. When swimming occurred, the direction was recorded as being either upward (toward the surface of the water) or downward (toward the bottom of the aquarium). Thirty individuals of each species were tested, including both sexes and a variety of size classes.

### Predation

The following procedure tested for predatory selection upon large (length > 15.0 mm) and small (length < 13.0 mm) *Idotea urotoma* by *Thalassoma lucasanum*. A 79-litre aquarium was divided in half, using a sheet of opaque plastic. An opaque plastic pipe was placed in the centre of each half of the tank as a barrier between prey and predator. One *Thalassoma*, which had been deprived of food for 24 h, was then transferred into each compartment, and allowed to acclimate for a 2 h period. Isopods of the same colour morph and sex were selected, and their length measured using a stereomicroscope with an ocular micrometer. Body length was determined as the distance to the nearest 0.5 mm from the anterior margin of the head to the posterior margin of the pleotelson (in dorsal aspect). To eliminate behavioural differences (e.g. swimming *v.* nonswimming) between individuals, isopod prey subjects were killed in hot water immediately before each feeding trial. At the start of each experiment two isopods (one large, one small) were placed in a head-head parallel alignment within the plastic pipe. The barrier was removed when the predator (*Thalassoma*) was determined to be in a neutral position. During each replicate test the fish was allowed to eat both isopods to control for predator fixation on a particular prey size class. To further avoid the possibility of a learning component, four individual *Thalassoma* were used in twenty feeding trials, each predator thus being used only five times. The size difference between the two isopod prey items, per trial, ranged from 4.0 to 7.5 mm, with a mean of 4.8 mm (s.d. = 0.40). Fish predators ranged in size (standard length) from 10.5 to 12.0 cm, with a mean length of 11.4 cm (s.d. = 0.18).

The same procedure was employed to determine whether or not a difference exists in predatory preference (selectivity) between *Idotea urotoma* and *Colidotea findleyi* of equal lengths. Twenty-four replicates were performed with prey ranging from 9.0 to 20.5 mm; fourteen of these trials were conducted with prey items shorter than 15.0 mm. One large (12.5 cm) and one small (9.5 cm) *Thalassoma* were tested.

The effect of behavioural differences between the two isopod species on predator

preference was examined by combining elements of the swimming–nonswimming behaviour experiment and the prey selection experiments. Five *Thalassoma*, deprived of food for 24 h, were placed in a 79-litre aquarium, and allowed to acclimate for a 2 h period. Pairs of equal length, same sex and colour, *Idotea urotoma* and *Colidotea findleyi* were placed in a 10 cm petri dish containing filtered seawater, and allowed to remain undisturbed for a 1 min acclimating period. Each dish was then lowered beneath the surface of the water simultaneously releasing the two isopods. Records were kept as to which species was consumed first, although in each trial both prey items were allowed to be eaten. This procedure was replicated nine times with 10 min periods between trials.

Fish predators ranged in size from 9.5 to 12.5 cm, with a mean length of 11.1 cm (s.d. = 0.49). The prey items ranged in length from 13.5 to 17.5 mm, and six of the replicates were between individuals below 15.0 mm. The number of replicates was determined by the availability of *Colidotea findleyi*.

### Morphometric analysis

All ten rocky shore species of Idoteidae that occur occasionally or principally in the Gulf of California were examined during this study. Specimens for this study came from the Crustacea collections of the Allan Hancock Foundation, Scripps Institution of Oceanography, and California Academy of Sciences. Length measurements were made to the nearest 0.5 mm in the dorsal aspect using either a stereomicroscope with an ocular micrometer or a dial caliper. Sample size to ascertain maximum body length and minimum reproductive size was determined by the maximum number of available specimens. Length–width analysis, because of its consistent relationship, was determined from a maximum of fifty individuals per species, and excluded ovigerous females due to width variations caused by differences in the number of eggs being brooded. Correlation coefficients and regression of width on length were computed using the standard library of a Texas Instruments 58c calculator. Differences in the slopes of the regression lines between species (i.e. differences in length/width ratios) were deter-

TABLE 1. Behavioural observations of isopods. Numbers are observed replicates distributed into proper categories.

	'Nonswimmers'	Upward 'swimmers'	Downward 'swimmers'	Total
<i>Idotea urotoma</i>	13	9	8	30
<i>Colidotea findleyi</i>	3	18	9	30

mined by analysis of covariance at the 0.01 level (Snedecor & Cochran, 1978).

## Results

### Behaviour

*Colidotea findleyi* exhibited locomotory activity in 90% of the trials (Table 1), and is thus categorized as a 'swimmer' (binomial test;  $P < 0.001$ , two-tailed). Only 57% of the *Idotea urotoma* manifested swimming behaviour, and data analysis indicates that this species can statistically be considered equally a 'swimmer' or a 'nonswimmer' (binomial test;  $P = 0.58$ , two-tailed). However, there is a significant difference between the distribution for the behavioural categories of the two species ( $\chi^2 = 12.7$ ;  $df = 1$ ). The 'nonswimmer' individuals of *I. urotoma* that passively drifted

downward assumed a characteristic posture, with their entire body arched upward and the second antennae rotated to their maximum posterior position or extended anteriorly parallel to the lateral margins of the body.

### Predation

In our experiments, in every case, *Thalassoma lucasanum* consumed whichever prey item was first touched. When presented with a choice between large and small motionless *Idotea urotoma*, *Thalassoma* significantly ate the larger isopod first in 80% of the replicates (binomial test;  $P = 0.024$ , two-tailed) (Table 2). *Thalassoma* also preferentially selected motionless *I. urotoma* over *C. findleyi* of equal length (binomial test;  $P = 0.022$ , two-tailed) (Table 3). However, there was no significant

TABLE 2. Size selective predation by *Thalassoma lucasanum* on large and small *Idotea urotoma*. Asterisk denotes individual eaten first; fish predator no. 1 was 12 cm S.L., no. 2 was 12 cm S.L., no. 3 was 10.5 cm S.L., no. 4 was 11 cm S.L.

Trial number	Size of small individual (mm)	Size of large individual (mm)	Colour phenotype†	Predator number
1	11.0	16.5*	dk brn	1
2	13.0	17.5*	dk brn/wh	2
3	10.0	15.5*	tan	1
4	11.0	16.5*	tan	2
5	11.0*	15.0	tan	1
6	12.0	17.0*	tan	2
7	9.0	16.5*	tan	1
8	10.5	16.0*	dk tan	2
9	10.0	15.0*	dk tan	1
10	11.0*	16.0	dk tan	2
11	10.5	15.0*	tan	3
12	11.5*	16.0	tan	4
13	12.0*	17.0	dk tan	3
14	11.5	16.0*	dk brn	4
15	12.0	16.0*	dk tan	3
16	12.0	16.5*	tan	4
17	11.0	16.5*	dk brn	3
18	12.0	17.0*	dk brn/wh	4
19	11.0	15.0*	dk brn/wh	3
20	12.0	16.0*	dk tan	4

† dk = dark; brn = brown; wh = white spots.

TABLE 3. Species selective predation by *Thalassoma lucasanum* on *Colidotea findleyi* and *Idotea urotoma* of the same length. Asterisk denotes individual eaten first; fish predator no. 1 was 12.5 cm S.L.; no. 2 was 9.5 cm S.L.

Trial number	Isopod size (mm)	<i>Colidotea findleyi</i>	<i>Idotea urotoma</i>	Predator number
1	18.0		*	1
2	13.0		*	2
3	20.5		*	1
4	10.0		*	2
5	13.0		*	1
6	12.0	*		2
7	9.0	*		1
8	15.0	*		2
9	20.0		*	1
10	13.0	*		2
11	17.0		*	1
12	12.0	*		2
13	17.0		*	1
14	16.5		*	2
15	16.5		*	1
16	11.0		*	2
17	14.0		*	1
18	10.0		*	2
19	12.5		*	1
20	11.0		*	2
21	12.0		*	1
22	16.0		*	2
23	13.0	*		1
24	15.5		*	2

difference in the degree of prey selectivity when comparing size preference to species preference ( $\chi^2 = 0.16$ ;  $df = 1$ ). This would seem to indicate that for *Thalassoma lucasanum* selection of prey is equally dependent on prey size and prey species (at least with respect to *Idotea* and *Colidotea*). There was also a significant preference for live *Idotea urotoma* versus live *C. findleyi* of equal length, when combining elements of the behavioural and predation experiments (binomial test;  $P = 0.020$ , one-tailed) (Table 4).

#### Morphometrics

An equatorward transition exists within the Idoteidae in which there is: (1) an increase in body ornamentation; (2) a general decrease of maximum body size; (3) a decrease in minimum size for onset of reproduction in females (Table 5). A comparison of body ornamentation between Gulf of California inhabiting temperate-derived *v.* tropical/sub-tropical-derived species reveals that 100% of

TABLE 4. Species selective predation by *Thalassoma lucasanum* on live *Colidotea findleyi* (= C) and *Idotea urotoma* (= I)

Trial number	Isopod size (mm)	Species eaten first	'Non-swimmers'	'Swimmers'
1	13.5	I	I	C
2	13.5	I	I	C
3	17.5	I	I	C
4	17.5	I		I and C
5	16.0	I	I	C
6	13.0	I	I	C
7	14.5	C	I	C
8	12.5	I	I and C	
9	14.5	I	I	C

the latter have body spination and/or cephalic humps and spines. In comparison, only 17% of the Gulf inhabiting temperate-derived species are ornamented. Minimum size to onset of brooding (in females) for eastern Pacific subtropical and tropical species is 4.5–10.5 mm, whereas for temperate species that occasionally inhabit the Gulf of California, minimum size to brood is 13.0 mm or greater. Of all northeastern Pacific idoteids considered, temperate species have the greatest maximum body length, ranging from 23.0 to 58.5 mm; subtropical species range in maximum body length from 17.5 to 24.5 mm; tropical species range from 11.5 to 12.0 mm.

There exists a strong correlation between body length and width in all species examined in this study ( $r = 0.90$ – $0.99$ ; Table 6). Arranging the species in a north to south fashion reveals a distinct trend in length to width ratios (Tables 6 and 7). *Colidotea findleyi* and *Erichsonella cortezi* are essentially restricted to the subtropical Cortezian province and have a significantly different slope to their regression lines when compared (with one exception, *I. resecata*) to species that have their principal ranges outside the Cortezian province (e.g. *Idotea* spp., *Parasymmerus* and *Eusymmerus*). Yet there are no significant differences ( $P \leq 0.01$ ) in regression analysis among the subtropical Cortezian *C. findleyi* and *E. cortezi* ( $F = 4.86$ ,  $df = 1.82$ ), or among the tropical species of *Eusymmerus* and *Parasymmerus* and some of their temperate equivalents (e.g. *Idotea* and *Synidotea*) (Table 7). In other words, body shape of *C. findleyi* and *E. cortezi* are more similar to each other than to other temperate or tropical species, and most

TABLE 5. Comparison of rocky shore Idoteidae (Isopoda) whose principal or occasional range includes the Gulf of California

Species	Minimum body length to brood (mm)	Maximum body length (mm)	Ornamentation (spines and/or cephalic humps)	Zoogeographic range*			
				Tropical	Sub-tropical	Warm temperate	Cold temperate
<i>Parasymmerus annamaryae</i>	4.5 (n = 11)	11.5 (n = 44)	Yes or No†	++	++		
<i>Eusymmerus antennatus</i>	5.0 (n = 12)	12.0 (n = 38)	Yes	++	++	+	
<i>Synidotea harfordi</i>	6.5 (n = 4)	17.0 (n = 15)	No	+	+	++	
<i>Colidotea findleyi</i>	7.0 (n = 124)	24.5 (n > 500)	Yes		++	+	
<i>Erichsonella cortezi</i>	10.5 (n = 13)	17.5 (n = 61)	Yes		++		
<i>Idotea urotoma</i>	13.0 (n > 500)	26.5 (n > 500)	No		+	++	++
<i>Idotea wosnesenskii</i>	13.0 (n = 74)	37.0 (n = 373)	No		+	++	++
<i>Idotea resecata</i>	14.0 (n = 84)	57.0 (n = 389)	No		+	++	++
<i>Idotea aculeata</i>	18.0 (n = 3)	23.0 (n = 13)	Yes or No†		+	++	++
<i>Idotea stenops</i>	37.0 (n = 11)	58.5 (n = 84)	No		+	++	++

\* Principal range = ++; occasional occurrence = +.

† Body ornamentation absent in northern populations, present and increasingly developed in equatorward populations.

TABLE 6. Regression of width on length (and correlation coefficients) for rocky shore idoteid isopods occurring principally or occasionally in the Gulf of California

Species	Regression line equations	Correlations coefficients	N
<b>Tropical</b>			
<i>Parasymmerus annamaryae</i>	= 0.3426(X) + 0.1331	0.98	20
<i>Eusymmerus antennatus</i>	= 0.2908(X) + 0.1787	0.90	35
<b>Subtropical</b>			
<i>Colidotea findleyi</i>	= 0.1126(X) + 0.2513	0.90	50
<i>Erichsonella cortezi</i>	= 0.1572(X) + 0.0489	0.96	36
<b>Temperate</b>			
<i>Synidotea harfordi</i>	= 0.2380(X) + 0.6074	0.91	12
<i>Idotea aculeata</i>	= 0.2289(X) + 0.1185	0.91	16
<i>Idotea resecata</i>	= 0.1969(X) + 0.2894	0.99	50
<i>Idotea stenops</i>	= 0.3368(X) + 0.6145	0.99	50
<i>Idotea urotoma</i>	= 0.2216(X) + 0.3170	0.95	50
<i>Idotea wosnesenskii</i>	= 0.2836(X) + 0.6196	0.97	50

of the principally temperate and tropical species tend to be relatively more similar in body shape to one another than they are to these two endemic species.

**Discussion**

Our predation experiments demonstrate that the tropical wrasse *Thalassoma lucasanum*,

within the size class of 9.5–12.5 cm, prefers to eat the larger of two possible isopod prey items within the tested size range of 9.0–20.5 mm. Both experiments using heat-killed prey substantiate this conclusion. *Idotea urotoma* may have been preferred in the between-species choice experiment because it has a body surface greater than *Colidotea findleyi* per equal length (as evidenced by the difference in the slopes of their regression lines;

TABLE 7. F values comparing the slopes of regression lines for rocky shore idoteid isopods occurring principally or occasionally in the Gulf of California. Asterisk denotes significance at  $P = 0.01$ ; analysis of covariance.†

	<i>Eusymmerus antennatus</i>	<i>Colidotea findleyi</i>	<i>Erichsonella cortezi</i>	<i>Synidotea harfordi</i>	<i>Idotea aculeata</i>	<i>Idotea resecata</i>	<i>Idotea stenops</i>	<i>Idotea urotoma</i>	<i>Idotea wosnenskii</i>
Tropical									
<i>Parasymmerus annamaryae</i>	0.01 (1,41)	66.64* (1,66)	95.38* (1,52)	3.22 (1,28)	3.38 (1,32)	35.62* (1,66)	0.04 (1,66)	16.29* (1,66)	1.24 (1,66)
<i>Eusymmerus antennatus</i>		69.07* (1,81)	59.11* (1,67)	3.93 (1,43)	3.62 (1,47)	52.04* (1,81)	0.07 (1,81)	17.87* (1,81)	1.93 (1,81)
Subtropical									
<i>Colidotea findleyi</i>			4.86 (1,82)	39.73* (1,58)	31.04* (1,62)	17.29* (1,96)	39.98* (1,96)	39.62* (1,96)	43.91* (1,96)
<i>Erichsonella cortezi</i>				29.85* (1,44)	19.78* (1,48)	3.64 (1,82)	20.02* (1,82)	20.99* (1,82)	22.36* (1,82)
Temperate									
<i>Synidotea harfordi</i>					0.08 (1,24)	21.16* (1,58)	1.63 (1,58)	3.37 (1,58)	0.24 (1,58)
<i>Idotea aculeata</i>						11.10* (1,62)	1.76 (1,62)	1.29 (1,62)	0.54 (1,62)
<i>Idotea resecata</i>							227.21* (1,96)	14.62* (1,96)	110.93* (1,96)
<i>Idotea stenops</i>								14.53* (1,96)	5.40 (1,96)
<i>Idotea urotoma</i>									8.12* (1,96)

† Degrees of freedom listed under F values in parentheses.

Table 7). These data compare favourably with other studies that have demonstrated size selective predation by fishes which locate their prey by a combination of factors including body length, width, shape and surface area (Ivlev, 1955; Brooks & Dodson, 1965; Hall, Cooper & Werner, 1970; Strong, 1972; O'Brien, 1975; Van Dolah, 1978; Cook, 1979; Nelson, 1979a, b). Van Dolah (1978), working with salt marsh fauna, concluded from laboratory experiments that *Fundulus heteroclitus* strongly selected for larger amphipods. Strong (1972) demonstrated that minimum size of maturity in female amphipods is lower in populations permanently subjected to predation, as compared with predator-free populations. Both Cooper (1965) and Nelson (1978) showed that decrease in mean size of reproductive females, within a

single season, occurs in amphipods due to predation. Nelson's (1979a) laboratory studies also showed size selective predation, and he concluded that larger individuals of the pinfish *Lagodon rhomboides* preferred to eat large amphipods, and conversely that smaller individuals preferred smaller amphipod prey. The difference in feeding strategies was attributed to size limitation in the predator's ability to handle the prey. Werner & Hall (1974) obtained similar results with foraging behaviour of the bluegill sunfish. Observations during the feeding trials of the present study clearly indicated that the size range of predators used had no difficulty in handling the size of prey we used.

The behavioural difference between the subtropical and temperate isopods investigated during this study may reflect different strate-



gies in avoiding predation by fishes. The adaptative advantage of being a 'swimmer' species, like *C. findleyi*, may be based on a compromise between time spent in the water column and body size. Isopods and other varieties of epifaunal organisms are often swept by currents and surge from their substrate, the resultant individuals in the water column being more conspicuous to fish predators. This is especially true for members of cryptic genera like *Colidotea* and *Idotea*, whose well-developed pigmentation enhances their visibility in the water. Freshwater planktivorous fishes have been shown to locate their cladoceran prey by pigmentation rather than body size selection (Zaret, 1972; Zaret & Kerfoot, 1975; Kettle & O'Brien, 1978). A corresponding view of the adaptive significance of 'nonswimmer' behaviour is to consider it a mechanism for mimicking fragments of marine plants that are drifting toward the bottom. In the intertidal zone at Point Fermin, California, it is nearly impossible during rising tides to distinguish between 'nonswimmer' *I. urotoma* and pieces of decaying surfgrass (*Phyllospadix scouleri*) that are being swept about between the rocks (personal observation). *Idotea urotoma*, like other idoteids, possesses a variety of colour phenotypes, and several of these match the colour of decaying *Phyllospadix*. Jansson & Matthiesen (1971) also noted 'nonswimming' behaviour in *Idotea* - *I. baltica* assumes a position similar to 'nonswimming' *I. urotoma*, while *I. chelipes* rolls into a ball while sinking to the bottom. Therefore smaller, narrower (more streamlined), fast swimming epibenthic macrocrustacea may dart through the water with low risks of discovery because of their rapid movement and small size. Larger and slower swimming organisms, however, may find it advantageous to remain motionless, drawing as little attention as possible to their presence. Such evolutionary strategies are not unexpected, and have been suggested for a variety of taxa other than crustaceans, particularly echinoderms (e.g., Lawrence, 1975; Nelson & Vance, 1979). Glynn *et al.* (1979) provided experimental evidence suggesting that increased levels of fish predation results in smaller-sized, behaviourally distinct populations of the tropical sea urchin *Eucidaris thousarii* (in Panama and Ecuador). Further studies of

pigmentation, size and shape of tropical and temperate epibenthic Crustacea are needed to elucidate evolutionary trends in morphology and locomotion.

The results of the predation experiment examining preference between live *I. urotoma* and live *C. findleyi* of equal body length are somewhat more difficult to interpret. One conclusion suggested by the data is that the combination of size and proximity to predators is more important in prey location than is passive versus active prey movement. *Idotea urotoma* used in our experiments sank closer to the predators than did the upward swimming *C. findleyi*. It is possible that the fish, in their 24 h starved state, would have tried to consume any floating object. Therefore, mimicking floating algae had little if any adaptative advantage under these artificial conditions. O'Brien (1979) has reviewed the importance of reactive distance (the minimum distance at which the predator can locate a specific prey) of planktivorous fish and noted that it was the most crucial element in locating crustacean prey. A second factor worth considering is the possible role of body ornamentation in prey selection. Several modifying factors probably interact with this predator-prey system in its natural environment. Predator distribution, prey density, fish grazer density, and density and complexity of algal substrate are some of the more obvious of these (see Earle, 1972; Menge & Sutherland, 1976; Glasser, 1979; Lobel, 1980). Nevertheless, the live prey experiment did continue to show the trend of the previous prey selection experiments in which the larger (in this case, wider) prey item was consistently consumed first.

#### *Zoogeographic and evolutionary considerations*

The northeast Pacific is a complex meteorological and hydrographic area composed of eight biogeographic provinces, in four regions (Briggs, 1974; Brusca & Wallerstein, 1979b) (Fig. 1). Separating the temperate Californian province from the tropics is a zone of overlapping subtropical and warm-temperate faunas along the shallow warm bays and cool rocky promontories, respectively, that exist from central to southwest Baja California.

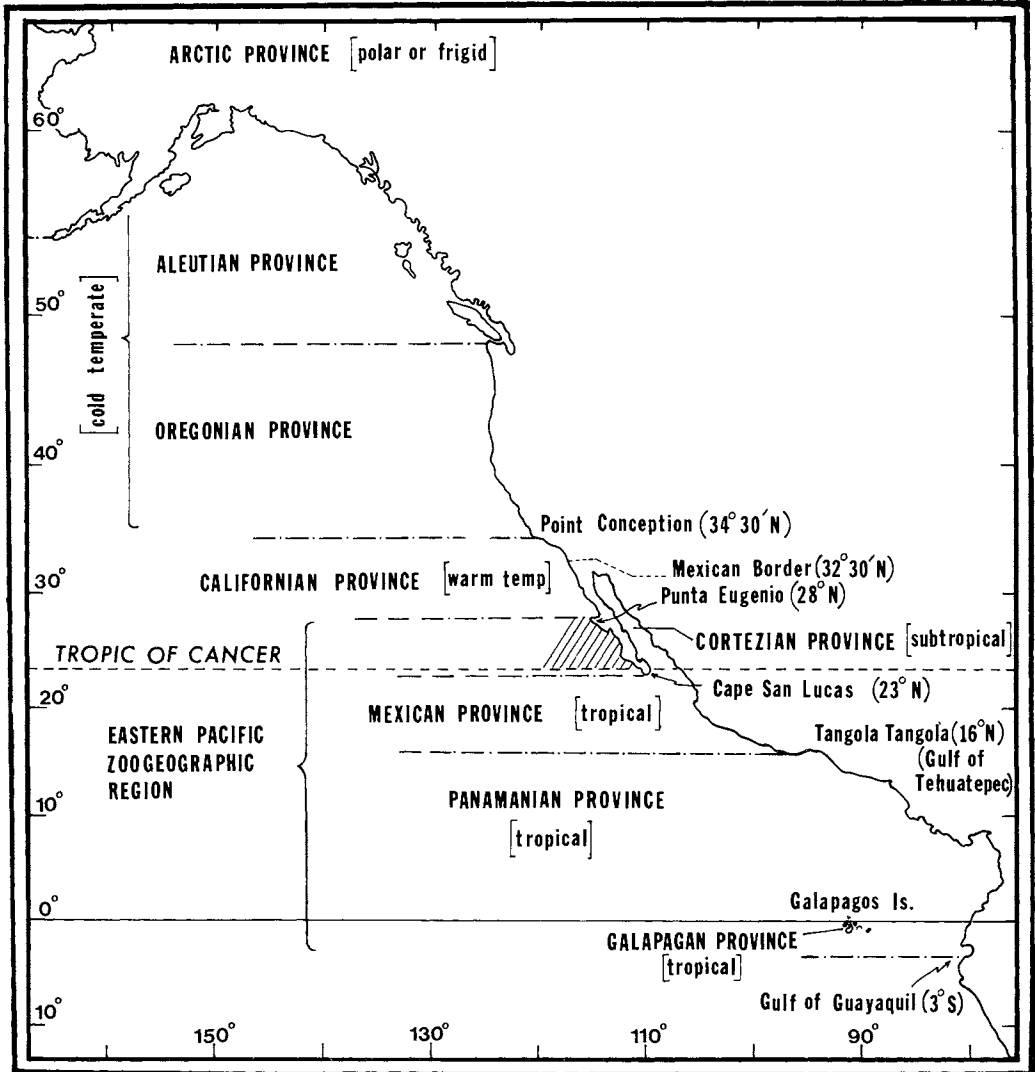


FIG. 1. Biogeographic coastal provinces of the northeast Pacific. (From Brusca & Wallerstein, 1979b.)

Brusca & Wallerstein (1979b) noted that the family Idoteidae is a cool to cold water centred taxon in the northeast Pacific, but that several genera penetrate significantly into the subtropical waters of northern Mexico. Presently, eight genera are known to inhabit or penetrate into the warm Cortezian and Mexican provinces. These are *Cleantoides*, *Colidotea*, *Edotea*, *Erichsonella*, *Eusymmerus*, *Idotea*, *Parasymmerus* and *Synidotea*.

Most authors consider temperature tolerance, current patterns, predation, and com-

petition as the major regulating forces governing distributions of marine organisms, with abiotic factors playing the pre-eminent role determining broadscale latitudinal ranges (e.g. Hutchins, 1947; Ekman, 1953; Briggs, 1974), while biotic factors have been shown to be of major importance in directing smaller-scale distributions within communities (e.g. Connell, 1970, 1975; Paine, 1971, 1974; Dayton, 1971, 1975; Dayton & Hessler, 1972; Menge, 1976; Menge & Sutherland, 1976; Lubchenco & Menge, 1978; Pielou, 1979; Nelson, 1980b).

In many instances the Idoteidae appear to present a contradiction to the generally accepted hypothesis that temperature is the primary regulatory mechanism of large-scale, latitudinal, marine biogeographic distributions. For example, most northeast Pacific members of the genus *Idotea* transverse four zoogeographic provinces and the associated temperature barriers to adjacent fauna (Brusca & Wallerstein, 1979b). Experimental data also show that the critical thermal maxima of two California populations of *Idotea urotoma* are nearly equivalent to the warmest temperatures found within the Cortezian province (Brusca & Wallerstein, 1979b; manuscript). These results are not unexpected since many authors have noted the plasticity of temperate intertidal species in adapting to extreme temperatures (Gunter, 1957; Segal, 1961; Kinne, 1963, 1970; and others). Based on these data, and the assumption that some or most species of wide-ranging *Idotea* possess the common characteristic of a clinal increase in temperature tolerance with decreasing latitude, it is reasonable to argue that temperature is not necessarily the primary factor governing the southern limit of wide-ranging intertidal species in this isopod family.

Experimental and observational data suggest that fish predation, acting as the proximal but persistent governing factor, is a more likely alternative hypothesis. The three morphological trends previously described for the northeast Pacific idoteid fauna are clearly related to a latitudinal gradient; there is strong correlative data suggesting that a corresponding trend of increasing fish predation pressure in low latitudes exist (Hiatt & Strasburg, 1960; Bakus, 1964, 1969, 1981; Hobson, 1965; Newman, 1960; Vermeij, 1978), especially on crustaceans. For example, Hobson (1968) found that of forty-six species (in twenty-four families) of predatory fishes he studied in the southern Gulf of California, only six did not rely, at least in part, on Crustacea. Thomson & Lehner (1976) reported that crustaceans were the principal food items for six of the ten dominant northern Gulf rocky intertidal fishes and noted that of the remaining four species, crustaceans comprised 10–50% of their diet. Talbot (1965) found that 61% of the fishes at Tanzania's Tatia Reef were carnivores. A num-

ber of other studies have shown the predominance of Crustacea in the diets of tropical fishes (Randall, 1967; Hobson, 1974; Lowe-McConnell, 1979; Matthey & Reynolds, 1979; Vivien, 1973). Based on experimental data from our studies, and current literature on prey selectivity by fishes, it appears reasonable to deduce that a reduction in both minimum reproductive size and overall body surface area would be a highly advantageous adaptive strategy for subtropical–tropical epifaunal macrocrustaceans. Further, noncrustose tropical algae are generally smaller than their temperate equivalents (Bakus, 1969), which increases the visibility of larger algal-inhabiting invertebrates. Because size of prey affects predatory selection, macrocrustaceans may also be subjected to a greater number or variety of predators as they grow. The observation that colder water temperatures are responsible for the occurrence of larger individuals in higher latitudes has often been invoked to explain size differences between northern and southern populations or species. However, Nelson (1980a), studying seagrass beds, found no significant difference in infaunal amphipod size among geographical areas, whereas epifaunal amphipods were significantly larger at his northern sites, which were inferred to be less predation-intense, indicating that predation not water temperature was probably responsible for size differences in these amphipod assemblages.

It is of particular interest that *Colidotea findleyi* and *Erichsonella cortezi* are essentially restricted to the northern Gulf of California (Brusca & Wallerstein, 1977). A number of authors have noted that this region possesses a distinct biotic assemblage within the Sea of Cortez (Garth, 1955; Thomson & Lehner, 1976; Brusca, 1980, 1982). The area is characterized by the presence of numerous disjunct Californian warm-temperate species and northern Gulf endemics. This consideration lends added significance to the fact that *C. findleyi* and *E. cortezi* have larger minimum sizes to reproduction than do their confamilial ecological equivalents that occur predominantly from the central Gulf southward. In fact *C. findleyi* and *E. cortezi* are the most frequently encountered idoteids in the northern Gulf, the former being a common and abundant member of the *Sargassum* community, whereas

*E. cortezi* (with a larger minimum reproductive size) is less abundant but present year-round (Brusca *et al.*, manuscript). The relative densities of these two species may reflect the relationship between predation pressure and their minimum reproductive sizes, even though both species have approximately the same fecundity.

Menge & Sutherland (1976) commented on the potentially important effects of temporal heterogeneity in permitting prey species to escape predation, listing winter in temperate and boreal regions, summer in deserts, and gales, as examples. The strong seasonality and periodic 'winter kills' in the northern Gulf may cause an annual decrease in the number of tropical fish species when compared to the central and southern Gulf ichthyofaunas (Thomson & Lehner, 1976; Thomson *et al.*, 1979). Hence, there may be a decrease in fish predation pressure in the northern Gulf that could be analogous to a trend moving northward along the outer coast of Baja California. If so, the lower temperature minima in the northern Gulf of California may make this region a significant refugium from fish predation pressure for cold-adapted and/or larger crustacean prey.

As seen in the morphometric analysis, species that have their principal range within the Californian or Mexican provinces have smaller length-to-width ratios than species that predominantly occur in the Cortezian province. In the lower latitudes idoteids become increasingly shorter in length, but broaden in the thoracic segments (e.g. *Parasymmerus* and *Eusymmerus*). The northern Gulf endemics in comparison are more elongate and in one species tubular in shape (*C. findleyi*). Temperate species generally possess a broad thorax and are large in size (e.g. *Idotea*). Menzies & Miller (1972) have noted that there is also a reduction in body size with decreasing latitude in the genus *Synidotea*. There are few exceptions to this latitudinal trend in the Idoteidae. One is *Colidotea rostrata*, a short, elliptical-shaped, species commensal on sea urchin spines; its southern range coincides with its temperate sea urchin host *Strongylocentrotus*. Another anomaly is a group of *Idotea* species that spends the major part of their adult life confined to the narrow blades of *Phyllospadix*

(Lee, 1972; Lee & Gilchrist, 1972). The general latitudinal pattern in the family suggests that there may be a decrease in body width and length with increasing predation pressure, until a lower limit in length is approached, where broadening can occur without a corresponding greater risk of predator discovery. Zimmerman (1978) found analogous results in the Amphipoda when comparing mean body size of a population from Catalina Island, California (33° 27' N, 118° 29' W), to an assemblage in the Gulf of California (27° N, 112° W). On the east coast, similar north to south patterns in Crustacea have been discussed in light of differential predation pressures at varying latitudes (Heck, 1979; Nelson, 1980a). Bakus & Green (1974) and Bakus (1981) have demonstrated a perhaps analogous trend of increasing toxicity in sponges and holothurians on an equatorward transition, concluding that fish predation had selected for noxious and toxic compounds within the tropics.

The latitudinal morphological patterns in the family Idoteidae show a clear trend of decreasing body width and length, and increasing body ornamentation at lower latitudes. We believe that reasonable evidence exists indicating this trend to correspond to an inferred trend of increasing predation pressure at lower latitudes. We are aware that better documentation of the latter trend is needed, despite the fact that considerable evidence exists in its favour. *Erichsonella cortezi* is the most highly ornamented idoteid in the northeast Pacific, possessing numerous large pereopod and pereopodal spines. Every North American congener of this species is ornamented to some degree, but decreasing ornamentation occurs in species whose populations are concentrated in the more northern latitudes. Two possible functions of ornamentation are that these structures help camouflage algal inhabiting isopods from predators, and secondly, spination may interfere with predator handling, and in some instances provide a negative stimulus to consumption.

The geological evolution of the region provides additional insight into the modern zoogeographic trends discussed above. Each of the North American Pleistocene Ice Ages caused a significant latitudinal shift in the position of coastal isotherms in respect to

the Baja California peninsula (Addicott, 1966; Wehmiller & Emerson, 1980). This series of oceanographic changes presumably produced a corresponding series of vicariant events, each of which could have been responsible for the establishment of warm-temperate disjunct (Californian–Cortezian) distributions, and the evolution of northern Gulf endemic species. Before the end of the last Ice Age, 8000–10 000 years ago, the Cortezian Province and the area of Mexico directly to the south were characterized by a temperate biota found within 20–22°C isotherms (McIntyre *et al.*, 1976). As the Ice Age drew to a close, the ensuing latitudinal rise of warm water isotherms (> 23°C) caused local extinctions of the majority of temperate species that occurred in the Sea of Cortez. Those temperate species able to adapt to warmer environmental regimes became isolated in the northern Gulf. Early passage of the Idoteidae into the north Pacific is indicated from distributional data and mid- to late Oligocene fossils in European deposits (Racovitza & Servastos, 1910). Species of *Idotea* and other temperate-derived idoteid taxa probably followed a generalized pattern for temperate biota (north–south–north range shifts), inhabiting the Gulf of California to some extent prior to each rising of the tropical isotherms. At present, periodic reinvasions of the warm Cortezian Province probably occur by rafting individuals that establish small, temporary, reproducing populations (e.g. *Idotea* spp. and *Synidotea harfordi*).

The causal factors that excluded permanent populations of large-bodied eurythermal Idoteidae from subtropical waters in the northeast Pacific at the end of the last Ice Age presumably depended on two mechanisms, which may have worked independently or in concert. Evolutionary rates of most temperate idoteid species may have proceeded too slowly to allow them to adapt to increasing water temperature, or predation pressure increased too quickly as the tropical faunal wave moved northward. If temperature acted as the excluding mechanism (with the rising coastal isotherms) and still is acting as a barrier, then two contradictions seem apparent. First, these highly eurythermal rocky shore species do occur occasionally in small reproducing colonies during the warmest parts of the year

in the subtropical Cortezian Province; and secondly, over the last 8000 years permanent reinvasion has not occurred, despite the high critical thermal maxima of at least some temperate populations. Thus, the more likely scenario is that the onslaught of northward-moving tropical predators arrived too quickly to allow the evolution of smaller body size in most temperate species. The northeast Pacific *Idotea* may have the genetic potential for evolving smaller body size to reduce predation pressure since a number of European species of *Idotea* start reproducing at sizes smaller than or equivalent to *Colidotea findleyi* (Sywula, 1964). *Synidotea harfordi* is an example of an eastern Pacific species that has evolved the capacity to reduce its reproductive size south of the Californian Province.

The fundamental hypothesis proposed in this paper is that fish predation has been and still is a significant factor controlling the extreme southern range of large bodied, rocky shore Idoteidae south of the Californian Province. Predation pressure also is hypothesized as having played a major role in moulding the evolution of morphologies within the family Idoteidae. The majority of tropical predatory fish distributions may be controlled by their temperature minima (Hubbs, 1948, 1960; Radovich, 1961; Fitch, 1967). Similarly, northern distributions of most tropical Idoteidae are hypothesized to also be regulated by minimum thermal tolerance (e.g. *Parasymmerus* and *Eusymmerus*). This presents us with an interesting picture of latitudinal distributions of coastal marine invertebrates that is analogous to the prevailing theory of vertical intertidal distribution, in which species' upper limits are controlled primarily by abiotic factors, while their lower limits are regulated primarily by biotic factors. Data revealed in these and other studies suggest that fish predation is an important component in structuring tropical communities, and that distinct differences observed in temperate and tropical epifaunal crustacean populations may be, in large part, a reflection of increased predation pressure in lower latitudes.

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