

Carnivore/non-carnivore ratios in northeastern Pacific marine gastropods

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ABSTRACT: For 2321 species of shelled gastropods of the northeastern Pacific, the ratio of carnivorous to non-carnivorous species (*C/NC* ratio), computed for each degree of latitude, reveals striking spatial changes, with tropical and arctic areas characterized by high values and with the mid-latitudes having the lowest ratios. This latitudinal trend is markedly different from trends for terrestrial clades. The zonal variation in *C/NC* ratios within bins is largely due to differences in geographic ranges of the groups; for example, tropical carnivorous species range farther than non-carnivorous ones, thus overlapping them in more latitudinal bins. Differences in the distribution and diversity of carnivorous and non-carnivorous species may arise from a number of sources, including variability of primary production in the tropical eastern Pacific, patchiness of substrates to which non-carnivores are adapted, narrow dietary specializations of tropical carnivores, and higher provinciality found in extratropical regions.

KEY WORDS: Trophic ratios · Latitudinal diversity trends · Provinciality · Variable productivity

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INTRODUCTION

Studies of latitudinal trends in diversity have largely focused on variations in species richness (for example Roy et al. 1994, 1998, Gaston & Williams 1996, Crame 2000, Gaston 2000) but changes in other aspects of biodiversity, such as compositions of local and regional faunas or the behavior of individual clades or functional groups, have remained underexplored. In particular, few data exist on latitudinal variations in the proportions of species belonging to different trophic types within regional or local marine faunas. A handful of studies have investigated carnivore/non-carnivore (*C/NC*) ratios in terrestrial clades, chiefly birds and beetles, and, with some exceptions, the consensus has been that these ratios within clades remain fairly constant among regions, perhaps with a decline at high

diversities (Faaborg 1985, Jeffries & Lawton 1985, Karr et al. 1990, Pimm 1991, Warren & Gaston 1992, Rosenzweig 1995). However, the evidence for near-constancy in the proportions of carnivore and non-carnivore species has often come from studies from similar climate zones and even from within single biogeographic provinces. When assemblages are sampled from regions that show large differences in environmental and biotic parameters or in evolutionary history, the *C/NC* ratio within a given clade may vary spatially or among environments (Wilson 1996). In beetles, for example, *C/NC* ratios vary among climatic zones (Gaston et al. 1992) and among islands with different histories, sizes and climates (Brinck 1948, Becker 1975, 1992).

Gastropods are among the dominant marine clades of the marine shelf benthos and are rich in both carnivorous and non-carnivorous species. Here, we examine patterns of the *C/NC* ratio in marine gastropods of the northeastern Pacific, from the tropics to the Arctic, and

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show that the ratio varies with climate and bathymetry. We also show that differences in the geographic ranges of carnivorous and non-carnivorous species within climatic zones play an important role in determining the regional variations. Note that because few carnivorous gastropods prey exclusively on other gastropods (e.g. Taylor & Taylor 1977), we are not dealing with predator/prey ratios as analyzed in community food webs and subwebs. Thus the energetic constraints imposed within trophic pyramids do not apply (see also Gaston et al. 1992, Warren & Gaston 1992). Instead, we are interested in the partitioning of diversity between primary and higher-level consumers for a major clade along a latitudinal gradient; these patterns of feeding-type ratios have evolutionary implications and potential ecological consequences of their own.

MATERIALS AND METHODS

We analyzed the diversity patterns of carnivorous and non-carnivorous species of shell-bearing marine gastropods ($N = 2321$ species) recorded on the continental shelf (above 200 m in depth) along the northeastern Pacific margin, from the southern edge of the Panamic province (Paita, Peru, 5° S) to the Arctic Ocean (off Point Barrow, Alaska, 72° N). Our distributional data consist of northern and southern range endpoints of individual species, and we assume that each species occurs continuously between those range endpoints (see Roy et al. 1998). A few clades were excluded because shells are absent or flimsy, so that they are likely to be poorly and unevenly represented in collections (such as most euthyneuran clades), or because they are so poorly understood taxonomically that their distributional records are untrustworthy (such as pyramidelids). We define as non-carnivores species that are browsers on marine plants, grazers that feed chiefly on algal or bacterial sources, detritus feeders (on the basis that most of their nutrition ultimately derives from algae or bacteria), and suspension feeders (on the basis that most suspended organic materials utilized are derived from algae or bacteria) (for references see Hawkins & Hartnell 1983, Levinton 1995). Our category of carnivores includes active predators and scavengers on animal tissue, consumers of sessile animals, such as sponges and cnidarians, and ectoparasites. Thus, we are, in practice, analysing latitudinal patterns in 2 trophic categories: primary consumers and consumers at all higher trophic levels. Finer resolution is not feasible, owing not only to the lack of specific information but to the dietary flexibility of many marine gastropods. Somewhat omnivorous species are assigned to their predominant trophic category. Our trophic assignments are summarized by family in Appendix 1.

In the ocean, many of the important variables that may affect the relative diversity of our 2 trophic categories change with depth (e.g. frequency and intensity of physical disturbance, available solar energy, overall biomass; see Rowe 1983, NOAA/NESDIS 1998). Thus we analyzed latitudinal C/NC trends in a number of discrete depth zones for each degree of latitude along the northeastern Pacific shelf. Depth categories used were: 0–1 m (essentially the intertidal fauna), 2–10 m (roughly to fair-weather wave base), 10–50 m (roughly to storm wave base) and 50–200 m (to the edge of the shelf). We assume that species are distributed in all zones between their minimum and maximum bathymetric distributions. Reliable bathymetric data are available for fewer species than are geographic range data; the bathymetric analyses are based on 1625 species.

The northeastern Pacific marine molluscan fauna is among the best-sampled in the world. However, the very small-bodied gastropods in the fauna, such as the vitrinellids, require special sampling methods and taxonomic expertise, and so their geographic distributions and diversity patterns may not be as reliable as those for larger species. Additionally, a number of species have very short recorded ranges (1° of latitude or less), and at least some of these may represent more wide-ranging forms that have been sampled at only 1 locality or a tight cluster of localities. If such a bias is non-randomly distributed in space then inclusion of such species could bias latitudinal trends in C/NC ratios. In order to test for size biases, we performed additional analyses excluding all species for which the geometric mean of length and height (a standard size metric for shelled mollusks, see for example Jablonski 1996, 1997, Jackson et al. 1996) was <5 mm, and recalculated C/NC ratio across latitudes. To test for artifacts arising from incomplete ranges, we excluded all 1° endemics and again recalculated the latitudinal trend in C/NC ratios. At least some short-ranging species may be genuinely restricted owing to adaptations to the unique conditions that prevail in the ecotones associated with biogeographic boundaries (see Newman 1979, Gofas 1998), but to be conservative all 1° species were omitted for this test.

RESULTS

The diversity (number of species) of shelled marine gastropods for each degree of latitude from the tropics to the Arctic Ocean is shown in Fig. 1A, with carnivore and non-carnivore diversities plotted separately in Fig. 1B,C. Two major regions stand out, tropical and extratropical, separated at Cabo San Lucas, near latitude 23° N. The most striking aspect of the pattern is

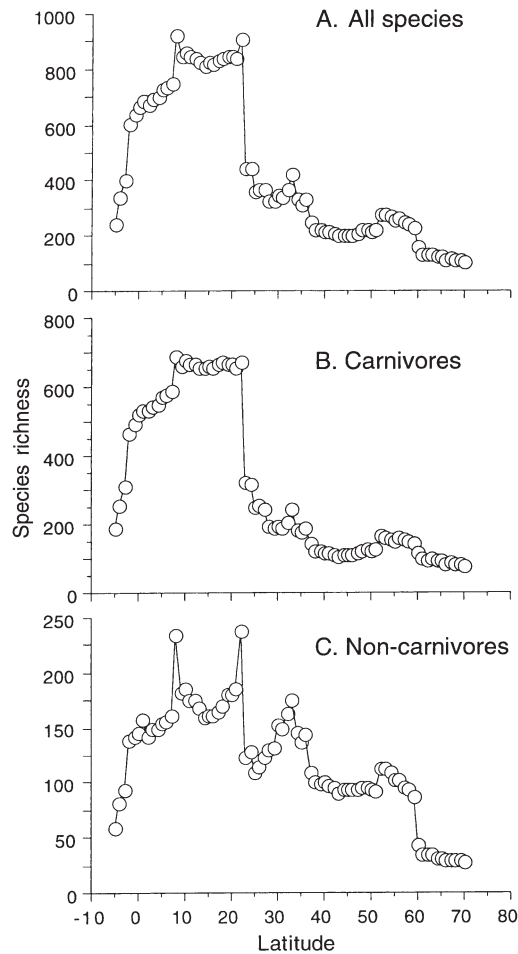


Fig. 1. Number of species of shelled gastropods present on the continental shelf within each degree of latitude from 5° S to 72° N in the eastern Pacific. (A) All species. (B) Species of carnivores. (C) Species of non-carnivores

that, while both groups show a positive latitudinal diversity gradient, the great diversity of the tropical gastropod fauna within 1° latitudinal bins is largely due to carnivores; non-carnivore diversity is only modestly higher in the tropics than in extratropical latitudes. The differences in the latitudinal distributions of the 2 trophic types when plotted at this spatial scale result in a distinctly non-linear trend in the C/NC ratio (Fig. 2). In general, the C/NC values can be divided into 3 blocks: (1) a tropical region with a high ratio that begins to decrease near the northern tropical margin, (2) a temperate region with much more equitable values of carnivores and non-carnivores and (3) an arctic region beginning near 60° N. Around 40° N the C/NC ratio approaches unity, but carnivore diversity accumulates more rapidly further south into the warm-temperate latitudes and is almost quadruple the non-carnivore diversity in each bin in the tropics. The carnivores

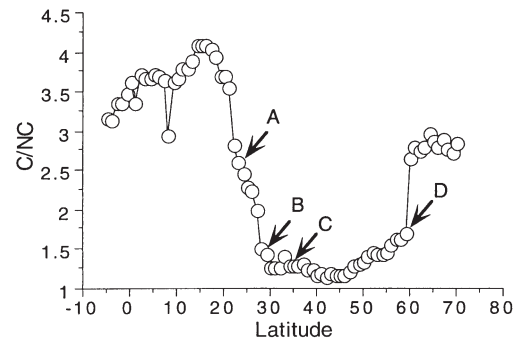


Fig. 2. Ratio of carnivorous to non-carnivorous species of shelled gastropods along the eastern Pacific shelf, binned as in Fig. 1. Note that the ratio varies with climatic zonation. The boundaries of marine molluscan shelf provinces are indicated by arrows: (A) Panamic-Surian; (B) Surian-Californian; (C) Californian-Oregonian; (D) Oregonian-Arctic

also outstrip non-carnivore diversity to the north of 40°, both groups showing a modest rise to a plateau near 50° N, and then losing diversity near 60°, but with non-carnivores showing a disproportionate drop so that carnivores dominate the depauperate gastropod fauna of the arctic, where the C/NC ratio within bins rises to within about 80% of its tropical value (Fig. 2).

Fig. 3 shows the C/NC ratios for a series of depth zones across the shelf. At all latitudes, the C/NC ratio approximately doubles from the shallowest to the deepest zone. The relative decline of non-carnivores with depth is expected, as the macroalgae, benthic microalgae, seagrasses and other primary producers that support many prosobranch species also decline (Lüning 1990, Markager & Sand-Jensen 1992). Despite these depth-related changes, the latitudinal pattern of C/NC values seen in the fauna as a whole holds within depth zones, with the temperate latitudes being relatively carnivore-poor, even in the deepest shelf zone where their representation is greatest within any given degree of latitude. We do note that due to sparser sampling offshore compared to shallow water, knowledge of bathymetric distributions is less reliable at greater depths, so patterns for the deeper zones should be interpreted more cautiously.

To test the robustness of the overall latitudinal trend in C/NC ratios, we reanalyzed the data excluding both the small-bodied species that are subject to greater sampling error (Fig. 4), and the species that are restricted to a single degree of latitude (data not shown). The patterns observed in the raw data clearly remain, although some discrepancies can be seen above 60° N, where species numbers are so low that the ratio is affected by small changes. One anomalous feature, a dip in the C/NC ratio around 8 to 9° N, is much reduced when 1° endemics are eliminated. We therefore at-

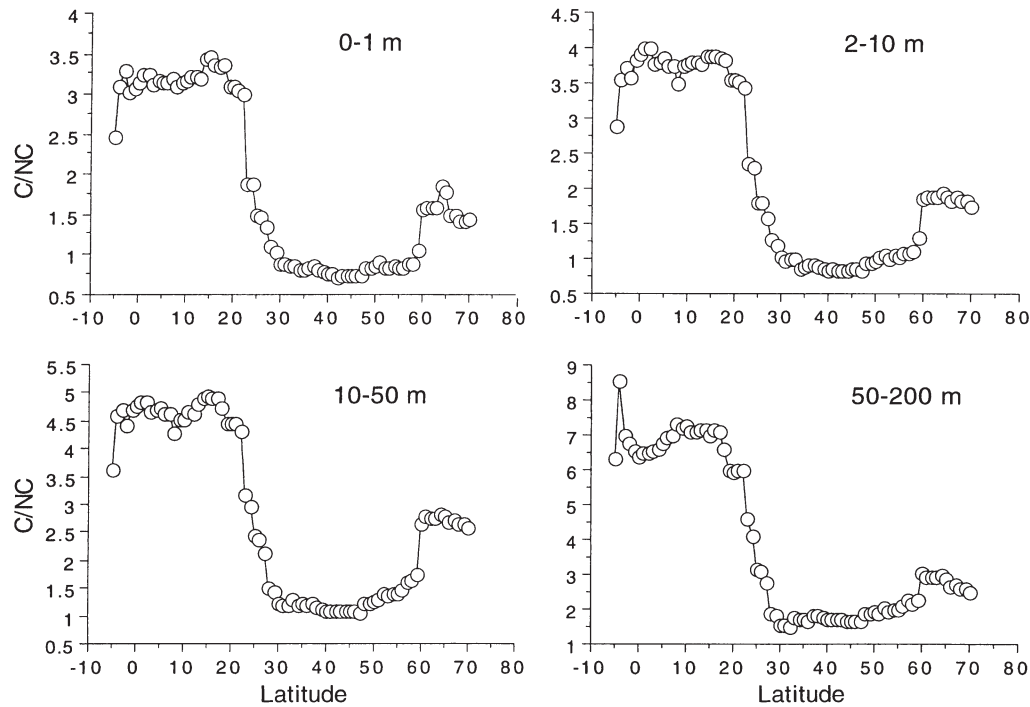


Fig. 3. Ratio of carnivorous to non-carnivorous species of shelled gastropods along the eastern Pacific shelf at 4 different depth zones, binned as in Fig. 1. The climatic zonation is clearly visible right across the shelf, although in the deeper zones the dominance of Arctic non-carnivores becomes muted. The number of species in the sample is quite small at Arctic latitudes, especially in deeper zones

tribute this anomaly to relatively heavy sampling around Panama, producing local records of many species that probably have wider geographic ranges but have yet to be collected on the less intensively explored shelves to

the north and south. The anomalously high peaks of molluscan diversity and range endpoints recorded at those same mid-tropical latitudes (Fig. 1A; Roy et al. 1998, 2000) are therefore also likely to be artifactual.

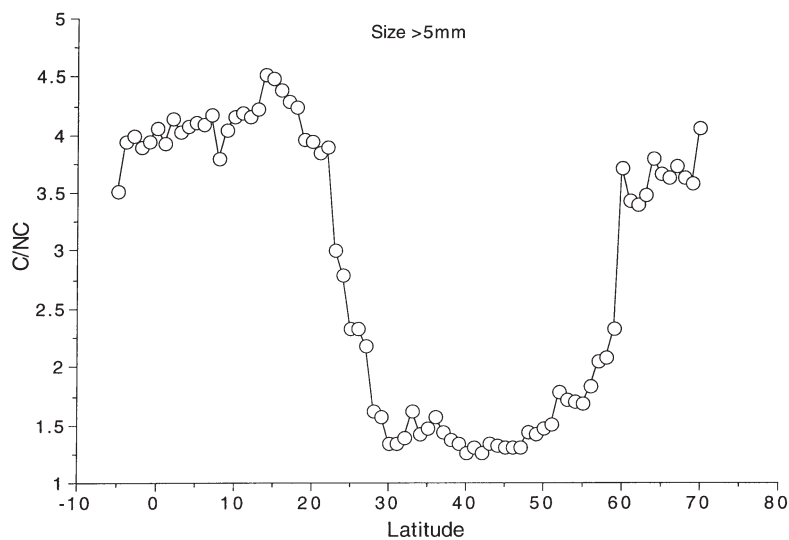


Fig. 4. Ratio of carnivorous to non-carnivorous species of shelled gastropods larger than 5 mm present on the eastern Pacific shelf, binned as in Fig. 1. The basic pattern is unaffected by removing small-bodied forms

Finally, the numbers of carnivorous species of gastropods in tropical and arctic waters are so substantial relative to non-carnivores that the differences are difficult to attribute simply to sampling, particularly in light of the preceding tests on the role of size and local variations in sampling intensity. In the tropics, the richness of carnivores exceeds that of non-carnivores by roughly 500 species, a difference unlikely to be erased by further collections, which would be as likely to yield new carnivores as non-carnivores (e.g. see Skoglund 1992). Similarly, although the absolute numbers are much lower in both trophic groups at high latitudes, the C/NC ratio within 1° latitudinal bins reaches a plateau at which carnivores outnumber noncarnivores by a factor of 3, again a difference unlikely to be eliminated by further collecting.

DISCUSSION

Latitudinal patterns and geographic range overlaps

Our results show impressive latitudinal variations in the relative proportions of carnivorous and non-carnivorous gastropods along the Northeast Pacific margin, with a zone of low C/NC ratios in the temperate regions relative to both tropics and arctic (Fig. 2). A qualitatively similar U-shaped latitudinal pattern was documented for the Northeast Atlantic by Taylor & Taylor (1977), using a very different approach based on local faunas, which suggests that the trend we observed in the Northeast Pacific is not unique to that system. In contrast, the latitudinal pattern of C/NC ratios in terrestrial beetles appears to be very different, with a larger proportion of carnivores in temperate latitudes than in the tropics (Gaston et al. 1992). Rosenzweig's (1995) summary, drawn from non-marine sources, also reports either constant C/NC ratios, or a decline with increasing diversity.

The latitudinal pattern in C/NC values, roughly coinciding with the broad climatic zonation of tropical, temperate and arctic regions, emerges when the data are plotted at a resolution of 1° latitudinal bins. However, when the latitudinal trends in C/NC are examined at the spatial scale of the 3 major regions delineated by the C/NC ratios in Fig. 2, the difference in C/NC ratios between tropical and temperate regions almost disappears (2.1 versus 1.9). Thus, for our data, the latitudinal trend in C/NC values depends on the spatial scale at which they are calculated. This contrast between the ratios within the large climatic regions and the C/NC trends found at a finer scale indicates that differences in the geographic ranges of carnivore and non-carnivore species play an important role in generating the latter trend.

To test for differential spatial turnover of carnivores and non-carnivores, we compared the within-region latitudinal ranges of each group for all 3 regions. As adjacent regions share many species, the important parameter here is how each species is distributed within a given region, and not its total range. Thus, for a species whose latitudinal range is split evenly between 2 adjacent regions, only half of its range contributes to the spatial turnover within each region. As shown in Fig 5., the biogeographic structure of the 2 trophic groups is indeed crucial in creating the finer-scale latitudinal trend in C/NC ratios. The carnivorous species have significantly longer within-region ranges in the tropics compared to the non-carnivores. Consequently, the tropical carnivore ranges overlap to a much greater degree, resulting in high diversity within any given 1° latitudinal bin. The tropical non-carnivore ranges are not only narrower, they are deployed such

that fewer species fall into a given 1° bin, resulting in a higher C/NC ratio at this spatial scale. In the temperate region, non-carnivore, within-regional ranges expand relative to their tropical within-regional ranges, and the carnivore range-frequency distribution resembles that of the non-carnivores (Fig. 5).

There are 2 issues in interpreting these carnivore and non-carnivore patterns. One involves the factors that are responsible for the very different C/NC ratio within a given degree of latitude in each of the climatic regions, for example the contrast in tropical ratios, near 4:1, with the much lower ratios found in temperate latitudes, between 2:1 and 1:1. The second issue involves the marked differences in geographic range between longer-ranged tropical carnivores and shorter-ranged tropical non-carnivores, and the removal of those differences in temperate regions.

Zonal controls

Major features of the distributional patterns of mollusks along the northeastern Pacific shelf are associated with the hydrographic framework. Provincial boundaries are located where waters of different major water masses or water types, conditioned in different climatic zones or representing mixtures of waters drawn from other distinctive sources, and distributed by currents, meet along the shelf (for example Dall 1921, Schenck & Keen 1936, Hall 1964, Valentine 1966, Gaylord & Gaines 2000). Previous studies have shown that provincial boundaries, formed by clusters of species-range endpoints, influence many aspects of northeastern Pacific molluscan biogeography (Roy et al. 1994, 1998), and the finding that the geographic ranges of carnivores and non-carnivores are different and vary regionally raises the possibility that they are associated with similar features. However, although regional climates affect both the provincial boundaries and the trends in C/NC ratios, changes in the C/NC ratios are not localized at provincial boundaries but proceed over 10° or so, while provincial boundaries associated with the margins of the tropic and arctic climate zones are relatively narrow and do not correspond to the breaks in slope of the C/NC ratio. Thus, there appear to be 2 distributional systems involved in the major geographic patterns of the prosobranch fauna. One system, of marine climate zones, is associated with gradients between regions of distinctive C/NC ratios that are partly based on differential range lengths in feeding types. This system corresponds to the zonal climates arising from variation in solar radiation. The other system, of molluscan provinciality, is associated with the localization of range endpoints at current and/or water-type convergences, so as to sepa-

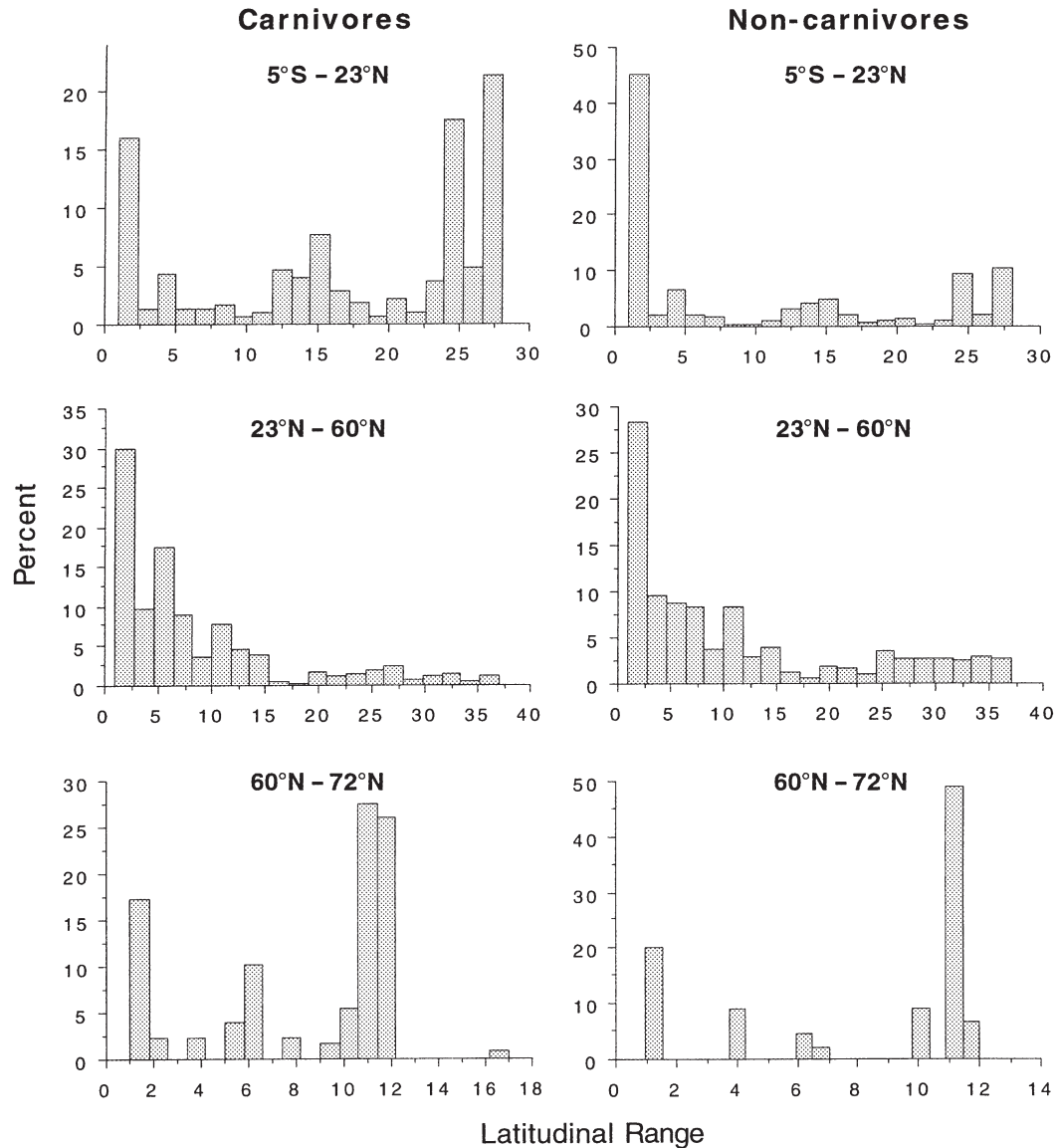


Fig. 5. Latitudinal range-length distributions of carnivorous (left panels) and non-carnivorous (right panels) species of shelled gastropods within each of the 3 zones of characteristic C/NC ratios: top, tropics; middle, temperate; bottom, arctic. Tropical carnivores have significantly longer ranges than tropical non-carnivores, so that although there are about 4 times as many carnivorous as non-carnivorous species in any degree of tropical latitude, the wide-ranging carnivores are only about twice as species-rich in the tropics as a whole

rate regions with distinctive faunal associations. This system corresponds to the regional shelf hydroclimates that are mediated by oceanic circulation. The provincial boundaries do show greater-than-average changes in C/NC ratios; however, this is particularly true of those boundaries located on the steeper portions of the C/NC curve, at 23° and 60°N, where waters conditioned in separate climatic zones converge (Fig. 2). Together, the zonal and provincial systems produce the major latitudinal trends in gastropod species associations.

Species richness and dietary breadth

One possible explanation for the diversity contrast within 1° bins from tropics to temperate regions is that dietary specialization in tropical carnivores permits more species to be supported within a given range of habitats. This hypothesis is supported by evidence that regional differences in relative diversities are accompanied by shifts towards broader feeding types at higher latitudes. For example, a single temperate species of the gastropod family Conidae can display a

range of diets that is wider than that of all tropical conid species combined (Kohn 1966, see also Taylor & Taylor 1977). The tropical carnivores are composed mainly of families that are overwhelmingly predatory, while about half of the arctic species belong to taxa that are more generalized feeders, such as the buccinids, which scavenge as well as take live prey (Taylor & Taylor 1977, Appendix 1 in present study). One interpretation of the trend toward generalists at higher latitudes is that the increasing seasonality of productivity favors species with broad diets that can forage in many habitats during inclement periods (for discussions see Valentine 1972, 1983, Taylor & Taylor 1977, Vermeij 1978, McClintock 1994).

Less is known of trophic partitioning within the non-carnivore clades (though see Hawkins & Hartnell 1983, as well as papers and references in John et al. 1992). The lack of a strong tropical diversity peak among non-carnivores may indicate that detritivores do not perceive much diversity among their food items. Obligate detritivores among the bivalves, approximate trophic analogs to the non-carnivore gastropods, do not exhibit a tropical diversity peak (Roy et al. 2000). In general, the grazing forms, including trochids and the fissurellid and acmaeid limpets, have more species in temperate waters than would be expected from the general molluscan latitudinal diversity gradient. This trend may reflect the rich algal macrophyte associations found in mid-latitudes, which, in addition to providing food directly, harbor abundant epiphytes and thus could provide enormous grazing areas and rich supplies of detritus. Northeast Pacific algal diversity peaks in the temperate rather than tropical latitudes when analyzed in 5° or 100 km bands (Gaines & Lubchenco 1982); and so the grazers may be tracking and partitioning the diversity of their trophic resources. However, in a global analysis of seaweed diversity, Bolton (1994) found no clearcut latitudinal trend. The high C/NC ratio at high latitudes is caused by a steeper reduction in the latitudinal species gradient of non-carnivores than of carnivores. This may be owing to increasing dietary breadth, or to the rigors of life in shallow arctic waters influenced by the effects of winter storms and ice.

Variability of primary production

Another possible explanation of the relatively low richness of non-carnivore species in the tropics of the eastern Pacific, not necessarily exclusive of the others, is that primary producers and therefore the non-carnivores are more heavily influenced by the coastal oceanography. Extensive and severe inshore upwelling of cold, deep water characterizes the tropical shelf

there, driven by winter winds arising from pressure differences between the Caribbean and the tropical Pacific (Alvarez et al. 1989, McCreary et al. 1989). Seasonal eddies and countercurrents have also been described or postulated for the main current (Costa Rica Coastal Current) over the shelf, though the dynamics remain unclear (see Badan-Dangon 1998). Overall, present evidence suggests that seasonality is unusually marked at tropical latitudes on the eastern Pacific shelf. The tropical segment of the eastern Atlantic, where the C/NC pattern is similar to that of the eastern Pacific, is famous for its coastal upwelling that produces considerable seasonal variability, the dynamics of which are still under study (see Ajao & Houghton 1998, Barton 1998, Shillington 1998). Such highly seasonal or otherwise episodic upwellings introduce nutrients into the euphotic zone and produce bursts of productivity, especially in low latitudes where levels of solar radiation remain relatively high throughout the year. Although species capable of exploiting such productivity bursts may be present in large populations, species richness is commonly lower in upwelling regions and in regions of high seasonality than in more stable areas (Thiel 1978, Alongi 1990), and significant upwelling effects have been recorded for other aspects of community structure as well (Menge et al. 1997, 1999). One test of the effects of variable upwelling would be to determine whether C/NC ratios along coastlines with subdued upwelling, such as the western Atlantic and western Pacific, exhibit the same U-shaped pattern seen in the eastern Pacific and eastern Atlantic.

C/NC range differentials

It has been postulated that the specialization of tropical species should produce narrow geographic ranges (Stevens 1989). However, for the tropical carnivorous gastropods, the postulated relatively narrow specializations are combined with relatively long ranges. If these carnivores actually have relatively narrow diets, then the narrow spectrum of food items that will support each of them is found across a relatively broad geographic range. While the geographic ranges of their food items are not known in any detail, bivalve species, common food items for predatory gastropods, have ranges in the tropics that are comparable to those of carnivorous prosobranchs (data not shown). It may also be that analogous latitudinal replacements of shorter-ranging prey species are readily available.

As to the relatively narrow ranges of tropical non-carnivores, a possibility is that those populations are more readily split than carnivore populations, owing to relatively narrow adaptation to substrates associated with their food sources, so that the contrast in geo-

graphic-range size might reflect the ease of range fragmentation. Many non-carnivores feed on microalgae, which may be patchy due to variation in substrates (see John et al. 1992). Patchiness of algae and non-carnivores might also reflect the patchiness in upwelling dynamics discussed above. Testing these suggestions requires data on the continuity of geographic ranges and habitats that are presently unavailable.

Provinciality may play a role in the differences in carnivore ranges between tropical and temperate zones. Within the tropical Panamic province there are no important faunal barriers, while extratropical provinciality is relatively high, several provincial and sub-provincial boundaries being recognized between 23° and 60° N (see Hall 1964, Valentine 1966, Gaylord & Gaines 2000). The consequent shortening of carnivore ranges in temperate latitudes creates a range-frequency distribution more similar to that seen in the non-carnivores, so that fewer carnivores are present in any 1° bin and the C/NC ratios decrease accordingly.

Historical factors

All of the preceding hypotheses relate to the present ecogeographical situation. However, over the past 5 million years the eastern Pacific has experienced major climate changes, faunal invasions and migrations, and faunal turnovers that have probably involved differential extinctions (Roy et al. 1996, Jackson et al. 1999, Smith 2000). Such changes have probably helped to shape the present biotic structure of the region, so that some of the parameters with which we are concerned reflect historical contingencies. Although differential turnover rates are known to occur among taxa, there is little evidence so far that the major diversity patterns discussed here have resulted from such differences. To be sure, there is a great variety of diversity patterns among lower taxa, but the high tropical diversities have clearly been achieved by the invasion or diversification of many small families, rather than having been imposed by a few dominant groups (see Roy et al. 1996). As the overall faunal patterns appear to be related to climatically based features to which many clades responded, any historical factors that have shaped them must have been climate-sensitive.

In marine invertebrates, narrow geographic ranges are generally associated with high extinction rates (Jablonski 1986, 1987). A potential macroevolutionary mechanism to produce tropical diversity differentials is for the more narrowly ranging tropical non-carnivores to have a significantly higher extinction rate, relative to speciation, than do tropical carnivores. The differential in the ratios between speciation and extinction in carnivores and non-carnivores must be smaller in tem-

perate latitudes, and there the range differences are smaller as well. Our latitudinal data are inadequate to define ranges at the highest latitudes, where many species have circumarctic distributions or, at least, ranges well beyond the Alaskan region. Unfortunately, knowledge of the geological ranges of gastropod species, particularly in the tropics, is still too fragmentary to permit direct calculation of turnover rates.

Summary and further considerations

The C/NC ratio shows a striking latitudinal pattern along the eastern Pacific shelf, with minimal values in the temperate zone and strong increases in both the tropics and the arctic. This pattern is qualitatively similar to that documented for the eastern Atlantic gastropods by Taylor & Taylor (1977), who used a very different approach based on discrete local and regional faunas. The pattern turns out to be underlain by the differential packing of species ranges into the major climatic zones along the shelf. These results show that the biogeographic deployment of major trophic groups within clades—and therefore their role in marine biotas—varies even for taxa that are major biotic constituents at all latitudes. Further work on underlying causes of these patterns, which might include quantifying differences in regimes of primary productivity, studying C/NC ratios along other latitudinal transects, and analyses of the evolutionary and biogeographic dynamics of species in the Plio-Pleistocene fossil record, should shed light on the mechanisms that structure trophic patterns within clades.

Our finding that the discordance between the C/NC ratio for the species pools of climate zones and the 1° scale is underlain by trends in the spatial packing of species should be tested at still finer scales. The community-level expression of the biogeographic differences between carnivores and non-carnivores may prove to be an important aspect of marine biodiversity along latitudinal gradients. Data are unavailable to test whether our macroecological, species-turnover interpretation of regional versus 1° patterns holds at the scale of local faunas or communities. However, we can say that the trends in C/NC ratios are not wholly habitat-specific, because the trends are maintained, albeit set at different levels, at 4 depth zones across the continental shelf (Fig. 3). Clearly, a comparative analysis of diversities within tropical and temperate molluscan communities would be a valuable step toward understanding how species are accommodated in these different regions.

Whether these within-clade patterns reflect latitudinal changes in the structure of benthic food webs is unclear. Despite a few important exceptions (e.g. Spight 1977, Lubchenco et al. 1984, Machado et al. 1996, Tay-

lor 1997 and references therein), most level-bottom benthic data are from the temperate zone, hindering comparative biogeographic analyses. Consequently we do not know whether the approximate proportionality of predator and prey species richness, such as found in a few marine communities by Warren & Gaston (1992),

breaks down in the tropics. Another important question is whether there is an association between biomass and C/NC ratios in food webs, Ricciardi & Bourget (1999) found higher community biomass in temperate rocky shore communities than at either higher or lower latitudes. Again, further analyses would be valuable.

Appendix 1. Gastropod families and feeding types. Taxonomy following Beesley et al. (1998). Feeding studies are unavailable for many of the species in our sample, but most families of marine gastropods are trophically homogeneous (Taylor & Taylor 1977). For families known to have mixed feeding strategies the dominant feeding type is listed here (c = carnivore, nc = non-carnivore)

Family	General feeding type	Reference	Family	General feeding type	Reference
Acmaeidae	nc	Boss (1982)	Obtortionidae	nc	Beesley et al. (1998)
Addisoniidae	nc?	Beesley et al. (1998)	Olivellidae	c	Morris et al. (1980)
Anabathridae	nc	Beesley et al. (1998)	Olividae	c	Taylor & Taylor (1977)
Architectonicidae	c	Beesley et al. (1998)	Orbitestellidae	nc	Beesley et al. (1998)
Assimineidae	nc	Fretter & Graham (1962)	Ovulidae	c	Beesley et al. (1998)
Barleeidae	nc	Fretter & Graham (1962)	Personidae	c	Taylor & Taylor (1977)
Batillariidae	nc?	Beesley et al. (1998)	Phenacolepadidae	nc	Beesley et al. (1998)
Buccinidae	c	Taylor & Taylor (1977), Shimek (1984)	Planaxidae	nc	Houbrick (1987)
Bursidae	c	Beesley et al. (1998)	Pleioptygmatidae	c	Quinn (1989)
Caecidae	nc	Beesley et al. (1998)	Pleurotomariidae	c	Beesley et al. (1998)
Calyptraeidae	nc	Boss (1982)	Potamididae	nc	Beesley et al. (1998)
Cancellariidae	c	Taylor & Taylor (1977)	Pseudococculinidae	nc	Marshall (1985)
Capulidae	nc	Beesley et al. (1998)	Ranellidae	c	Beesley et al. (1998)
Cassidae	c	Taylor & Taylor (1977)	Rissoellidae	nc	Beesley et al. (1998)
Cerithiidae	nc	Beesley et al. (1998)	Rissoidae	nc	Beesley et al. (1998)
Cerithiopsidae	c	Beesley et al. (1998)	Scissurellidae	nc	Boss (1982)
Cingulopsidae	nc	Beesley et al. (1998)	Seguenziidae	nc	Beesley et al. (1998)
Columbellidae	c	Taylor & Taylor (1977)	Siliquariidae	nc	Beesley et al. (1998)
Conidae	c	Taylor & Taylor (1977)	Skeneidae	nc	Beesley et al. (1998)
Coralliophilidae	c	Boss (1982)	Skeneopsidae	nc	Boss (1982)
Costellariidae	c	Beesley et al. (1998)	Strombidae	nc	Beesley et al. (1998)
Cypraeidae	c, primarily	Boss (1982)	Terebridae	c	Taylor & Taylor (1977)
Epitoniidae	c	Beesley et al. (1998)	Tonnidae	c	Beesley et al. (1998)
Eratoidae	c	Beesley et al. (1998)	Trichotropididae	nc	Boss (1982)
Eulimidae	c	Beesley et al. (1998)	Tricoliidae	nc	Boss (1982)
Fasciariidae	c	Taylor & Taylor (1977)	Triphoridae	c	Beesley et al. (1998)
Ficidae	c	Beesley et al. (1998)	Triviidae	c	Morris et al. (1980)
Fissurellidae	nc	Boss (1982)	Trochidae in part	nc	Hickman & McLean (1990)
Haliotidae	nc	Morris et al. (1980)	Trochidae Callio-	c	Hickman & McLean (1990)
Haloceratidae	c	Beesley et al. (1998)	stomatinae		
Harpidae	c	Taylor & Taylor (1977)	Trochidae Troch-	c	Marshall (1995)
Hipponicidae	nc	Beesley et al. (1998)	aclidinae		
Lamellariidae	c	Beesley et al. (1998)	Truncatellidae	nc	Beesley et al. (1998)
Lepetidae	nc	Yonge (1960), Angerer & Haszprunar (1996)	Turbinellidae	c	Beesley et al. (1998)
Littorinidae	nc	Beesley et al. (1998)	Turbinidae	nc	Beesley et al. (1998)
Marginellidae	c + nc	Taylor & Taylor (1977), deMaintenon (1999)	Turridae	c	Beesley et al. (1998)
Melongenidae	c	Taylor & Taylor (1977)	Turritellidae	nc	Allmon (1988), Allmon et al. (1992)
Mitridae	c	Taylor & Taylor (1977)	Vanikoridae	nc	Boss (1982)
Modulidae	nc	Beesley et al. (1998)	Vasidae	c	Taylor & Taylor (1977)
Muricidae	c	Taylor & Taylor (1977)	Velutinidae	c	Fretter & Graham (1962) Boss (1982)
Nassariidae	c, primarily	Cernohorsky (1984)	Vermetidae	nc	Morris et al. (1980, Boss (1982)
Naticidae	c	Taylor & Taylor (1977)	Vitrinellidae	nc	Moore (1972), Bieler & Mik- kelsen (1988), Ponder (1994)
Neptuneidae	c	Taylor & Taylor (1977)	Volutidae	c	Taylor & Taylor (1977)
Neritidae	nc	Beesley et al. (1998)	Volutomitridae	unknown	Beesley et al. (1998)
			Xenophoridae	nc	Boss (1982)

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