

and may also be preadaptive to photosynthetically functional kleptoplasty.

Precise relationships between Volvatellidae, primitive Elysioidea (parapodium-bearing taxa), and primitive Stiligerioidea are presently unclear. However, functional plastid retention appeared early in both the elysioid and stiligeroid lines, occurring in caulerpivorous elysiids and in caliphyllids feeding on siphonocladalean algae. Both these dietary patterns are apparently plesiomorphic in their respective clades (CLARK & BUSACCA, 1978; CLARK & DEFREUSE, 1987; NUTTALL, 1987). However, this does not solve the problem of the origin of functional kleptoplasty, for we do not know whether the Stiligerioidea and Elysioidea had a common shell-less ancestor, in which function first appeared, or whether these clades were derived separately from shelled, cladohepatic forms (probably volvatelloid), with convergent evolution of functional kleptoplasty in each line. Because the two major preadaptive changes, cladohepatic and supportive diverticular cells, appear precursorily in two families of Conchoidea, the change between non-functional and functional kleptoplasty may have involved a very small genetic change, such as partial suppression of immune recognition, or translocation of a few genes from plastid/plant to animal genome. CLARK & DEFREUSE (1987) suggested that functional plastid retention may have increased fitness among early shell-less forms by compensating for difficulty in feeding on calcified Siphonales.

Kleptoplastic abilities of two families remain uninvestigated: Platyhedylidae and Gascoignellidae. These highly modified shell-less forms have uncertain relationships with other families, and knowledge of their diets and kleptoplastid retention capabilities might clarify these. *Gascoignella aprica* Jensen, 1985, the only known gascoignellid, has dark green diverticula, but these are shielded by melanin pigment, a character usually associated with non-functional plastids, as in the black form of *Limapontia depressa* (HINDE & SMITH, 1974), and in *Ercolania fuscata* and *Elysia catulus* (present study).

Considered at the generic level, and excepting the primitive shelled species, GREENE's (1970b) perception of widespread distribution of functional kleptoplastids is probably the most appropriate view. The ability to maintain functional kleptoplastids occurs in most shell-less genera (though it may be absent in some species of a genus and among ecotypes). Its absence may be related to inappropriate plastid structure, and such other factors as light, temperature (STIRTS & CLARK, 1980), and life-history strategies (WAUGH & CLARK, 1986; CLARK & DEFREUSE, 1987). The widespread occurrence of functional kleptoplasty among Elysiidae should be considered primarily the result of retention of an evolutionarily conservative diet of siphonocladalean algae, and not an evolutionarily advanced condition.

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# Range Limits and Dispersal of Mollusks in the Aleutian Islands, Alaska

by

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*Abstract.* The Aleutian-Commander arc of islands linking Alaska and Kamchatka provides a dispersal corridor for North Pacific species. A biogeographical analysis of 109 shallow-water shell-bearing molluscan species collected during two expeditions to the Aleutian Islands has yielded several new westward range extensions of eastern Pacific species and some eastward extensions of western Pacific species. These include *Lottia digitalis* (Rathke, 1833), west to Kiska; *Opalia borealis* (Keep, 1881), west to Adak; *Nucella lamellosa* (Gmelin, 1791), west to Nizki; *Plicifusus stejnegeri* (Dall, 1884), east to Nizki; *Volutopsius pallidus* Tiba, 1973, east to Adak; and *Amphissa columbiana* Dall, 1916, west to Chuginadak. Aleutian and Bering Sea records of *Nucella emarginata* (Deshayes, 1839) are erroneous; this species (in the broad sense) reaches its northern limit somewhere between Yakutat, southeastern Alaska, and Kodiak Island in the northern Gulf of Alaska.

Contrary to the pattern in warm-water faunas, in which pelagic larval stages are linked to broad geographical ranges, Aleutian species with planktonically dispersing larval stages are not more likely to have wider east-west distributions (that is, to be distributed in a continuum across the North Pacific) than are species with nonplanktonic larvae.

## INTRODUCTION

The cool-temperate North Pacific Ocean supports an exceptionally rich biota that, despite a few episodes of extinction and of invasion from other faunas, has remained a distinct entity since at least late Eocene time. The two predominant biogeographical components are an eastern Pacific element, evolving on the American side, and a western Pacific element, evolving in Asia. During the late Paleogene and Neogene, these biotic components exchanged species through eastward and westward dispersal, with the result that many taxa came to be distributed on both sides of the North Pacific (KILMER, 1978; KAFANOV, 1984). Links between the eastern and western North Pacific seem

to have been especially strong during warm intervals of the middle and late Miocene (MARINCOVICH & KASE, 1986; MARINCOVICH, 1988) and, although many of these links have subsequently been severed as indicated by the existence of species pairs of eastern and western Pacific species in lineages with formerly continuous ranges across the North Pacific (KEEN, 1941; VERMEIJ, 1989), many species maintain a continuous range from east to west in the North Pacific today.

This link is most likely to be maintained along two corridors, the region of Bering Strait near the Arctic Circle, and the Aleutian-Commander chain of islands between the Alaska Peninsula and Kamchatka. For both corridors, dispersal across a water barrier is prerequisite for maintain-

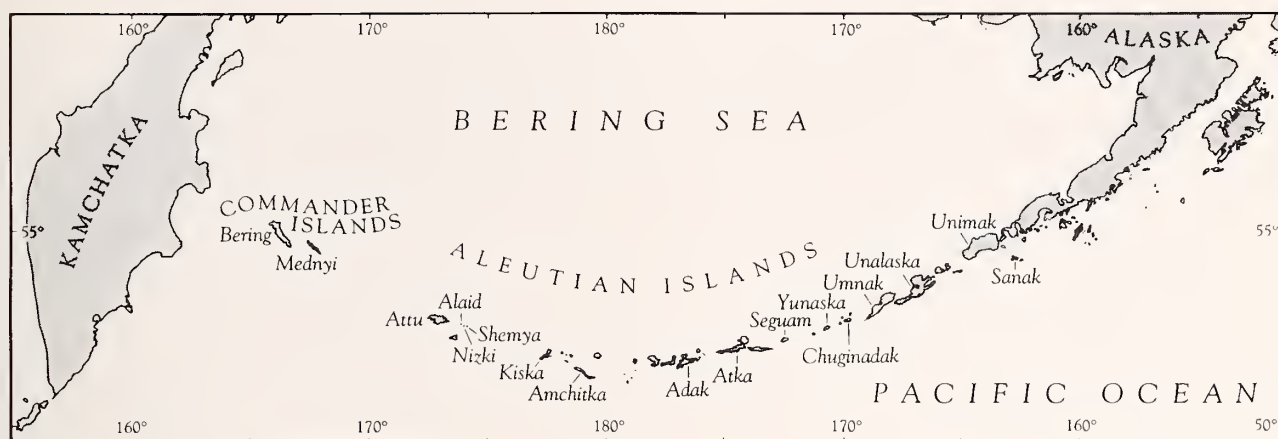


Figure 1

Map of Aleutian-Commander arc.

ing continuity of range. Such dispersal could occur by a planktonic larval stage or by rafting or floating at any stage in the life cycle. In some cases, the benthic adults may live in water deep enough that inter-island barriers do not inhibit dispersal.

A collecting expedition by Vermeij and Palmer aboard the R/V *Alpha Helix* to 11 of the Aleutian Islands during the summer of 1987 provided an opportunity to study range limits in relation to larval dispersal mode among common shallow-water shell-bearing mollusks. Several new eastern and western geographical range limits were established, which forced us to think about why some species fail to extend continuously across the North Pacific despite a pelagic dispersal phase. This paper is an outgrowth of our observations, together with an analysis of Lindberg's collections made at Attu in 1979.

#### MATERIALS AND METHODS

Mollusks were collected by hand in the intertidal zone and from rocky bottoms to a depth of 10 m at the following islands, listed from west to east (Figure 1): Near Islands (Attu, Nizki, Shemya), Rat Islands (Kiska and Amchitka), Andreanof Islands (Adak), and Fox Islands (Seguam, Yunaska, Chuginadak, Umnak, and Unalaska). The subtidal specimens were collected by D. O. Duggins, J. A. Estes, D. Irons, K. A. Miller, and J. Watson during field studies of sea otters and kelps (see DUGGINS *et al.*, 1989). Intertidal collections were made by Vermeij and Palmer. In 1979, Lindberg made intertidal and subtidal collections at Attu. His material, together with a few specimens of the 1987 expedition, is housed at the Los Angeles County Museum of Natural History; the rest is in the Vermeij collection.

Gastropods and pelecypods were critically examined and identified by Vermeij, Lindberg, Palmer, J. H. McLean, and R. Baxter. D. Ernisse kindly identified most polyplacophorans. Geographical range limits and distributions

were compiled from a critical survey of the literature (GOLIKOV & GULBIN, 1977; GOLIKOV & KUSSAKIN, 1978; KUSSAKIN & coworkers, 1978; LINDBERG, 1981, 1982, 1988; FOSTER, 1981; SCARLATO, 1981; BAXTER & MCLEAN, 1984; BAXTER, 1987; REID, 1989) and through inspection of the collections at the Los Angeles County Museum of Natural History and the U.S. National Museum of Natural History. Probable mode of larval dispersal was determined mainly from STRATHMANN (1987) and BERNARD (1979) and references therein.

#### RESULTS

A list of the 109 species of mollusks in our collections is given in Table 1, together with distributions in the Aleutian-Commander arc and inferred mode of larval dispersal. This number represents a minority of the molluscan species known from the Aleutians, but our species are biogeographically more or less typical of the fauna as a whole. Our critical review of BAXTER's (1987) compilation shows that 222 of the 396 shell-bearing molluscan species reported by him and by us from the Aleutians (56%) have ranges extending across the North Pacific from the mainland coast of Alaska to the mainland coast of Asia: 157 species (39%) are eastern Pacific species with their western range limits in the Aleutians, and 17 species (4.3%) are Asian species with their eastern limits in the Aleutians. The comparable percentages for our species are 71% (amphi-Pacific), 23% (eastern Pacific), and 5.5% (western Pacific). Our calculations from Baxter's lists must be treated with caution in view of many taxonomic and distributional uncertainties, especially for the deep-water species that Baxter included but that are unrepresented in our material.

Several of the species listed in Table 1 require comment. They are discussed in the following paragraphs.

*Puncturella longifissa* Dall, 1914. This northwestern Pacific species of keyhole limpet was previously recorded as

Table 1

Shallow-water marine shell-bearing mollusks collected in the Aleutian Islands. Key: +, ranging throughout Aleutian Islands; B, nonplanktonic larva; P, planktonic larva.

Species	Aleutian range	Larval type
Gastropoda		
<i>Anatoma obtusata</i> (Golikov & Gulbin, 1978)	+	B
<i>Puncturella</i> ( <i>P.</i> ) <i>longifissa</i> Dall, 1914	Adak west	
<i>P.</i> ( <i>Cranopsis</i> ) <i>major</i> Dall, 1891	Kiska east	
<i>Erginus</i> ( <i>E.</i> ) <i>puniceus</i> Lindberg, 1988	Attu west	B
<i>E.</i> ( <i>E.</i> ) <i>apicina</i> (Dall, 1879)	+	B
<i>E.</i> ( <i>Problacmaea</i> ) <i>moskalevi</i> (Golikov & Kussakin, 1972)	Unalaska west	B
<i>E.</i> ( <i>P.</i> ) <i>sybaritica</i> (Dall, 1871)	+	B
<i>Lottia borealis</i> (Lindberg, 1982)	+	P
<i>L. digitalis</i> (Rathke, 1833)	Kiska east	P
<i>L. ochracea</i> (Dall, 1871)	+	P
<i>L. painei</i> Lindberg, 1990	Attu east	P
<i>L. pelta</i> (Rathke, 1833)	+	P
<i>Rhodopetala rosea</i> Dall, 1872	+	B
<i>Tectura scutum</i> (Rathke, 1833)	+	P
<i>T. testudinialis</i> (Müller, 1776)	+	P
<i>Acmaea mitra</i> Rathke, 1833	Umnak east	P
<i>Cryptobranchia concentrica</i> Middendorff, 1847	+	P
<i>Margarites</i> ( <i>M.</i> ) <i>albolineatus</i> Smith, 1889	+	B
<i>M.</i> ( <i>M.</i> ) <i>beringensis</i> Smith, 1899	+	B
<i>M.</i> ( <i>M.</i> ) <i>helicinus</i> (Phipps, 1774)	+	B
<i>M.</i> ( <i>Valvatella</i> ) <i>pupillus</i> (Gould, 1841)	Umnak east	P
<i>M.</i> ( <i>V.</i> ) <i>vorticifer</i> Dall, 1873	+	B
<i>Homalopoma lacunatum</i> Carpenter, 1864	Attu east	
<i>Moelleria costulata</i> (Möller, 1842)	Attu east	
<i>Spiromoelleria quadrae</i> (Dall, 1897)	+	
<i>Lacuna</i> ( <i>Ephera</i> ) <i>porrecta</i> Carpenter, 1864	+	P
<i>L.</i> ( <i>E.</i> ) <i>vincta</i> (Montagu, 1803)	+	P
<i>Littorina</i> ( <i>Neritrema</i> ) <i>aleutica</i> Dall, 1872	+	B
<i>L.</i> ( <i>N.</i> ) <i>subrotundata</i> Carpenter, 1864	+	B
<i>L.</i> ( <i>N.</i> ) <i>sitkana</i> Philippi, 1846	+	B
<i>Onoba bakeri</i> (Bartsch, 1910)	Attu east	B
<i>O. dinora</i> (Bartsch, 1917)	Attu east	B
<i>O. cerinella</i> (Dall, 1886)	+	B
<i>O. kyskensis</i> (Bartsch, 1912)	+	B
<i>Boreocingula katherinae</i> (Bartsch, 1912)	+	
<i>Barleeia subtenuis</i> Carpenter, 1864	Attu east	B
<i>Cerithiopsis stejnegeri</i> Dall, 1884	+	
<i>Opalia borealis</i> (Keep, 1881)	Adak east	
<i>Melanella columbiana</i> (Bartsch, 1917)	Attu east	
<i>M. randolphi</i> (Vanatta, 1899)	+	
<i>Crepidula grandis</i> Middendorff, 1849	+	P
<i>Trichotropis</i> ( <i>Ariadnaria</i> ) <i>insignis</i> Middendorff, 1849	+	
<i>T.</i> ( <i>Turritropis</i> ) <i>cancellata</i> Hinds, 1843	+	
<i>Cryptonatica clausa</i> (Broderip & Sowerby, 1829)	+	B
<i>Velutina conica</i> Dall, 1887	+	P
<i>V. prolongata</i> Carpenter, 1864	Attu east	P
<i>V. velutina</i> (Müller, 1776)	+	P
<i>Fusitriton oregonensis</i> (Redfield, 1846)	+	P
<i>Boreotrophon truncatus</i> (Ström, 1788)	+	B
<i>Nucella canaliculata</i> (Duclos, 1832)	Attu east	B
<i>N. lamellosa</i> (Gmelin, 1791)	Nizki east	B
<i>N. lima</i> (Gmelin, 1791)	+	B
<i>Buccinum baeri</i> Middendorff, 1848	+	B
<i>B. glaciale</i> Linnaeus, 1761	+	B
<i>B. picturatum</i> Dall, 1877	+	B
<i>Volutharpa ampullacea</i> (Middendorff, 1847)	+	B
<i>Colus periscelidus</i> (Dall, 1891)	Sanak west	B

Table 1  
Continued.

Species	Aleutian range	Larval type
<i>Plicifusus stejneri</i> (Dall, 1884)	Nizki west	B
<i>Volutopsius pallidus</i> Tiba, 1973	Adak west	B
<i>Amphissa columbiana</i> Dall, 1916	Chuginadak east	B
<i>Astyris amiantis</i> Dall, 1919	+	B
<i>A. rosacea</i> (Gould, 1840)	+	B
<i>Oenopota harpularia</i> (Couthouy, 1839)	+	
<i>Evalea amchitkana</i> (Dall & Bartsch, 1909)	+	
<i>Philine polaris</i> Aurivillius, 1887	+	
<i>Liriola thersites</i> Carpenter, 1864	+	B
<b>Pelecypoda</b>		
<i>Crenella leana</i> (Dall, 1897)	+	
<i>Musculus discors</i> (Linnaeus, 1767)	+	B
<i>Mytilus (Pacifimytillus) californianus</i> Conrad, 1837	Amchitka east	P
<i>M. trossulus</i> Gould, 1850	+	P
<i>Modiolus modiolus</i> (Linnaeus, 1758)	+	P
<i>Vilasina vernicosa</i> (Middendorff, 1849)	+	
<i>Chlamy</i> sp.		
<i>Pododesmus macrochismus</i> (Deshayes, 1839)	+	P
<i>Diplodonta orbellus</i> (Gould, 1852)	+	
<i>Kellia suborbicularis</i> (Montagu, 1803)	+	P
<i>Rochefortia aleutica</i> Dall, 1899	Attu east	
<i>R. tumida</i> (Carpenter, 1864)	Attu east	
<i>Cyclocardia crebricostata</i> (Krause, 1885)	+	B
<i>C. incisa</i> (Dall, 1903)	Attu east	B
<i>Astarte bennetti</i> Dall, 1903	+	
<i>A. rollandi</i> Bernardi, 1858	+	
<i>Clinocardium nuttalli</i> (Conrad, 1837)	+	P
<i>Serripes laperousi</i> (Deshayes, 1839)	+	P
<i>Mactromeris polynyma</i> (Stimpson, 1860)	+	P
<i>Macoma calcarea</i> (Gmelin, 1791)	+	P
<i>M. expansa</i> (Carpenter, 1864)	Attu east	P
<i>M. sp. cf. M. obliqua</i> (Sowerby, 1817)	+	P
<i>Cadella nuculoides</i> (Reeve, 1844)	Attu east	P
<i>Peronidia lutea</i> (Wood, 1828)	+	P
<i>Siliqua alta</i> (Broderip & Sowerby, 1829)	+	P
<i>S. patula</i> (Dixon, 1789)	Attu east	P
<i>Protothaca staminea</i> (Conrad, 1837)	+	P
<i>Saxidomus giganteus</i> (Conrad, 1837)	Attu east	P
<i>Liocyma fluctuosa</i> (Gould, 1841)	+	
<i>Hiatella arctica</i> (Linnaeus, 1767)	+	
<i>Mya arenaria</i> Linnaeus, 1758	+	P
<i>M. truncata</i> Linnaeus, 1758	+	P
<i>Thracia myopsis</i> (Möller, 1842)	+	
<b>Polyplacophora</b>		
<i>Leptochiton rugatus</i> (Carpenter in Pilsbry, 1892)	+	
<i>Schizoplax brandti</i> (Middendorff, 1847)	+	
<i>Tonicella lineata</i> (Wood, 1815)	+	
<i>T. rubra</i> (Linnaeus, 1767)	+	
<i>Juvenichiton saccharina</i> (Dall, 1878)	+	
<i>Placiphorella borealis</i> (Pilsbry, 1893)	+	
<i>Mopalia ciliata</i> (Sowerby, 1840)	+	
<i>Katharina tunicata</i> (Wood, 1815)	Attu east	
<i>Cryptochiton stelleri</i> (Middendorff, 1847)	+	

far east as Amchitka (O'CLAIR, 1977). We have specimens from Amchitka as well as from Adak. Limpets were found at depths of 6–7 m on rocks and kelp blades. The Adak record is currently the easternmost limit of the species in the North Pacific.

*Lottia digitalis* (Rathke, 1833). This is an American limpet of the high intertidal zone. BAXTER (1987) recorded it as far west as Adak. During the 1987 *Alpha Helix* cruise, we found a population of very large individuals at North Point, Kiska. GOLIKOV & KUSSAKIN (1978) were inclined to doubt the record of *L. digitalis* from Avachin Bay, Kamchatka, which was based on empty shells. Accordingly, we regard Kiska as the westernmost record of *L. digitalis*. It is unlikely that these specimens represent a rare, fortuitous dispersal event as specimens collected in April 1974 are present in the collections of the University of Alaska Museum, Fairbanks, Alaska.

*Acmaea mitra* Rathke, 1833. In her compilation of Alaskan mollusks, FOSTER (1981) recorded an occurrence of this low intertidal and sublittoral limpet from Kiska. In our own surveys, we have found *A. mitra* only from Umnak east. Given the fact that the coralline-pavement habitats that are preferred by *A. mitra* are common and were carefully examined at all the islands visited, we are reasonably confident that *A. mitra* is absent or extremely rare west of Umnak. The Kiska record probably refers to *Erginus apicina* (Dall, 1879), a species very similar in appearance to the usually larger *A. mitra*. We therefore regard Umnak as the westernmost documented occurrence of this species.

*Margarites pupillus* (Gould, 1841). This common eastern Pacific trochid is abundant in the intertidal zone at Unalaska, and was found at depths of 6–7 m as far west as Umnak. Intensive searching in favorable low intertidal and sublittoral habitats on islands farther west failed to yield living or dead specimens.

*Littorina aleutica* Dall, 1872. This low-spined, often heavily sculptured species has often been confused with *L. sitkana* Philippi, 1846, but is in fact distinct (REID, 1989). It extends from the northern Kurile Islands to the Alaska Peninsula, and is common on most of the Aleutian islands we visited. Curiously, however, none of us has found it at Attu, and no material of *L. aleutica* is present in the large Aleutian holdings at the U.S. National Museum. Whether this absence represents a collecting artifact or a true absence is unclear.

*Trichotropis cancellata* Hinds, 1843. In Table 1 we have listed this species as extending continuously across the North Pacific from Asia to North America. In our collections, however, the species occurs only from Unalaska eastward. Although *T. cancellata* is reported from east Asia as well as from North America (GOLIKOV, 1986), the possibility that it has a discontinuous distribution cannot be eliminated on presently available evidence.

*Opalia borealis* (Keep, 1881). This large epitoniid is reported by DUSHANE (1979) as having its northern limit at Forrester Island in southeastern Alaska. We found living specimens at one intertidal and one shallow subtidal site

at Adak. These finds therefore represent a major westward extension of range for this species.

*Nucella canaliculata* (Duclos, 1832). It is remarkable that Soviet workers have not reported this common intertidal species from the Commander Islands or points farther west and south, because *N. canaliculata* is common at Attu (the westernmost of the Aleutians) and on all other islands we visited. O'CLAIR (1977) did not report the species from Amchitka, but we have found the species to be abundant there, and assume that O'Clair confused it with *N. lima* (Gmelin, 1791), which is also abundant throughout the Aleutians.

*Nucella emarginata* (Deshayes, 1839). Although we have not found this species in the Aleutians, we discuss it here in order to clarify the northern limit of this common eastern Pacific species. Elsewhere it will be shown (PALMER *et al.*, in press) that two species have been treated under the name *N. emarginata*, the southern or "true" *N. emarginata* from California and a northern species to which we shall, for the sake of convenience, refer as "northern" *N. emarginata*. DALL (1915) gave the range of *N. emarginata* (in the broad sense) as the southern Bering Sea and the Aleutian Islands south to northern Baja California. This range has been accepted by all later authors (*e.g.*, FOSTER, 1981; BAXTER, 1987). Inspection of the U.S. National Museum's collections upon which Dall based his conclusions show, however, that the Aleutian and Bering Sea records all refer either to *Buccinum baeri* or to *N. lima*. Palmer has collected *N. emarginata* at Yakutat, in southeastern Alaska. This is currently the northernmost valid record for the species.

*Nucella lamellosa* (Gmelin, 1791). In his review of North Pacific species of *Nucella*, DALL (1915) recorded *N. lamellosa* from the northeastern Pacific as well as from Sado Island in the Japan Sea. HABE (1958) followed Dall in accepting the western Pacific specimens as *N. lamellosa*, but GOLIKOV & KUSSAKIN (1962, 1978) regarded them as representing a distinct subspecies or species, *N. elongata* Golikov & Kussakin 1962. According to GOLIKOV & KUSSAKIN (1978), the range of this species is restricted to the southern Kurile Islands, Sakhalin, and the northern Sea of Japan. No specimens resembling *N. lamellosa* have been recognized by Soviet workers from the northern Kuriles, Kamchatka, or the Commander Islands (see also KUSSAKIN & coworkers, 1978). The previous western record for *N. lamellosa* is Adak (BAXTER, 1987). We have collected living specimens from as far west as Nizki, and have also found specimens at Adak and Umnak. The U.S. National Museum contains lots from Adak, Atka, and Unimak. Most of the specimens came from sublittoral rocks at depths of 6–7 m, but at Adak we found a few intertidal individuals. All the material we have seen from the Aleutians is strongly sculptured with axial frills, and the aperture is bordered by a thin lip unadorned with teeth. The smooth thick-lipped morphs so characteristic of the Puget Sound region apparently do not occur in southwestern Alaska.

*Plicifusus stejneri* (Dall, 1884). DALL (1884) described

this buccinid as *Strombella callorhina* var. *stejnegeri* from Bering Island in the Commander Islands, but he considered it possible that the new variety might be specifically distinct from his *S. callorhina* Dall, 1877, from the Pribiloff Islands. Soviet workers have justifiably considered it to be a distinct species, and have recorded it from the Commander and northern Kurile Islands (GOLIKOV & GULBIN, 1977). Our record from depths of 6–7 m at Nizki is believed to be the first reported occurrence of the species from Alaskan waters. *Plicifusus stejnegeri* differs from *P. kroeyeri* (Möller, 1842) by the higher spire, thicker outer lip, and especially by the axial ribs, which are much coarser and farther apart; *P. stejnegeri* differs from *P. callorhinus* by stronger and more closely spaced axial folds and by the higher spire.

*Volutopsius pallidus* Tiba, 1973. It is surprising that Dall and other early naturalists did not find this species in the Aleutians, for it is commonly found living in shallow subtidal waters, and also occurs as empty shells on beaches. We have specimens from as far east as Adak. In the Kuriles and in eastern Hokkaido, *P. pallidus* occurs at a depth of several hundred meters (TIBA, 1973; OKUTANI *et al.*, 1988). The smooth white shell distinguishes it from all other species of *Volutopsius*. We are persuaded that *V. pallidus* is not merely a pale deep-water variety of *V. middendorffi* (Dall, 1891), as OKUTANI *et al.* (1988) speculated.

*Amphissa columbiana* Dall, 1916. FOSTER (1981) recorded this large eastern Pacific columbellid from the Chia-chi Islands off the south coast of the Alaska Peninsula and from the western Gulf of Alaska. BAXTER (1987) did not report the species from the Aleutians. In our survey, we found *A. columbiana* from Chuginadak eastward at depths of 6–7 m.

*Mytilus californianus* Conrad, 1837. In our surveys, this mussel was found to be common in the intertidal zone from Umnak eastward. We found a single small but extremely thick-shelled specimen at Seguam, and O'CLAIR (1977) reported a single specimen from Amchitka. All Aleutian specimens we have seen are remarkable for the very faint development of the radial folds that are so prominent in specimens in southeastern Alaska and farther south (see also VERMEIJ, 1989).

## DISCUSSION

In his analysis of the shallow-water mollusks of Amchitka, O'CLAIR (1977) recognized 3 endemics (species restricted to the Aleutian and Commander islands), 5 Asian species, and 10 North American species among the 40 he collected from that island in the central Aleutians. As more biogeographical data have become available, however, it is increasingly clear that no molluscan species are endemic to the Aleutian-Commander arc. *Littorina aleutica*, for example, is now known to extend from the mainland coast of Alaska to the northern Kurile Islands (REID, 1989). *Astyris amiantis* (DALL, 1919), also regarded by O'Clair as endemic, occurs from mainland Alaska to the Kuriles

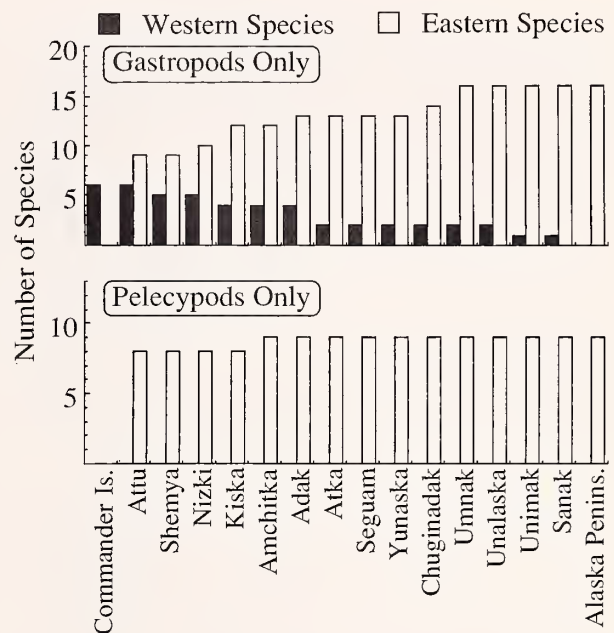


Figure 2

Patterns of disappearance of eastern and western Pacific species whose range boundaries occur somewhere within the Aleutian-Commander arc. Species occurring throughout the arc are not included. The height of the bar for each station along the arc indicates the number of species occurring at least that far east (solid bars) or west (open bars).

and to the island of Moneron in the Sea of Japan (GULBIN, 1983). Several of the species regarded by O'Clair as Asiatic (*Rhodopetala rosea*, *Onoba castanella* Dall, 1886, and *Cerithiopsis stejnegeri*) similarly have a continuous North Pacific distribution from North America to Asia. *Spiromoelleria quadrae* and *Littorina kurila* (as *L. atkana* Dall, 1896), classified as North American by O'Clair, again have continuous North Pacific ranges (BAXTER & MCLEAN, 1984; REID, 1989).

Nevertheless, the evidence at hand indicates that the Aleutian chain contains the endpoints of range of many species. Of the 109 species (67 gastropods, 33 pelecypods, and 9 polyplacophorans) recorded in Table 1, 25 (16 gastropods, 8 pelecypods, and 1 polyplacophoran) reach their western limit somewhere in the Aleutians, and 6 (all gastropods) reach their eastern limits there (Figure 2). Attu (the westernmost of the Aleutians) is the western limit for 10 gastropods, 6 pelecypods, and 1 polyplacophoran, and the eastern limit for 1 gastropod. Some of these limits (especially those at Attu) will likely be changed as more collecting is done. Some of them may even shift with changing oceanographical conditions from year to year. Figure 2 shows that, with the exception of the range limits at Attu, the diminution of American species westward along the chain is almost exactly compensated by the addition of Asian species. At least one additional species (the pul-



Table 2

Distribution of planktonic and nonplanktonic development among biogeographical categories of Aleutian gastropods.

Category	Planktonic species	Non-planktonic species	% species with planktonic larvae
Continuously ranging across North Pacific	12	24	33%
Western limits in Aleutians	4	7	36%
Eastern limits in Aleutians	0	5	0%

monate limpet *Liriola thersites*) reaches its western limit in the Commander Islands west of Attu (KUSSAKIN and coworkers, 1978). Species with continuous North Pacific distributions represent 71% (77 of 109 species) of the Aleutian shallow-water molluscan fauna.

The literature on geographical range in relation to dispersibility suggests that species with planktonic dispersal stages generally have larger geographical ranges than do species lacking such stages (see *e.g.*, HANSEN, 1978). Although there are exceptions, this relationship generally applies to tropical mollusks (see *e.g.*, PERRON & KOHN, 1985). At high latitudes, however, many species with nonplanktonic larval stages nevertheless achieve very broad geographical ranges (ARNAUD, 1974; CANTERA & ARNAUD, 1984; HIGSMITH, 1985), presumably because the larvae or even the adults are able to float or are transported on rafts of seaweed or wood.

Of the 52 gastropod species for which we were able to infer mode of larval dispersal, 35 have nonplanktonic stages and 17 have a planktonic phase (Table 1). Among the 35 species without planktonic larvae, 11 (31%) have eastern or western range limits within the Aleutian-Commander arc. The comparable figure for planktonically dispersing species is 29% (5 of 17 species), a number not significantly different from the 33% for nonplanktonic dispersers (*G*-statistic with Yates Correction,  $P > 0.10$ ). The bivalves show a similar pattern; 20% of the species without planktonic larvae have range endpoints within the Aleutian-Commander arc, compared to 25% with planktonic larvae.

These data imply that, although there is a slight tendency for planktonic dispersal to be associated with a continuous east-west distribution across the North Pacific, the water barriers between islands in the Aleutian-Commander chain are nearly as effective for planktonically dispersing species of gastropods as for species that lack planktonic life stages. This interpretation, however, may be somewhat complicated by the fact that the incidence of nonplanktonic development among species within western limits in the Aleutians (7 of 11 species, 65%) is lower than that among species reaching their eastern limits in the

Aleutians (5 of 5 species, 100%) (Table 2). The number of species is too small to determine if this difference between American and Asian gastropods is statistically significant. Future studies may have to take geographical origin into account in analyses of the relationship between range and dispersibility. Too few species had range endpoints within the Aleutian-Commander arc to conduct this analysis for pelecypods.

It is surprising that the Aleutian-Commander arc presents a barrier for many northeastern Pacific species with pelagic larval stages. The westward-flowing Alaska Stream along the south coast of the Alaska Peninsula and the Aleutian Islands (MCALISTER & FAVORITE, 1977) can potentially transport pelagic larvae of North American species westward. Moreover, there appears to be no obvious thermal or other oceanographical barrier along the island arc that could serve to limit the range of pelagically dispersing species. MILLER & ESTES (1989) described a similar paradox for the large bull kelp *Nereocystis luetkeana*, which has been seen living as far west as Umnak but which washes ashore (after westward transport) as floating plants at Attu and even in Hokkaido.

The possibility exists that the biogeographical barriers along the mainland coasts of Alaska and Siberia are just as effective, and act in the same way, as do the inter-island barriers in the Aleutian-Commander arc. Because detailed knowledge of range endpoints of species is lacking in many cases, especially in western Alaska, this interesting possibility cannot be examined further at this time.

In our analysis, we evaluated dispersibility of species by correlating inferred larval type with the distribution across barriers along a specific island arc, in which the number and size of such barriers are known. This method, which was also used by VERMEIJ (1987) in a study of over-water dispersibility of gastropods across water barriers in the tropical Pacific, differs from the more conventional method of comparing larval type against the total geographical ranges of species, as was done by HANSEN (1978) and by many others. The disadvantage of assessing dispersibility by means of whole ranges is that the precise range limits are often poorly known. The latitudinal and longitudinal extent of range, however, is very sensitive to the precise delimitation of distributional endpoints. By focusing on whether species can cross specific barriers, this problem is alleviated at least to some extent.

That the water barriers in the North Pacific have been more or less effective for millions of years is implied by the fact that a large number of eastern Pacific genera, most of which are known back to Oligocene time, are unknown as fossils or as living species in the western Pacific. Examples of such genera in the Aleutian fauna include *Opalia*, *Amphissa*, *Mytilus* (*Pacifimylus*) (for *M. californianus*), and *Crassidomus* (for fossil records see BERNARD, 1986; KAFANOV, 1987). Whatever the explanation for the effectiveness of the barriers, the phenomena responsible for the barriers should be observable throughout much of the Neogene.