seeds are small and thin-walled with slightly elongated surface cells. The arrangement of the floral parts is shown in Fig. 2*a*, *b*.

The organization and structure of the fossil flower suggest a close relationship to a number of Recent genera of the Saxifragales. Diplostemonous flowers are known within the Saxifragales, although obdiplostemony or haplostemony is the common organization of the androecium. Unilocular and inferior ovaries are also found in a number of saxifragalean families. Free, pendant placentae, however, are not common, and have only been observed in a few genera. Although all characters known to occur in the fossil flower are found within the saxifragalean complex, no modern genus seems to possess exactly the same combination of characters as the fossil flower. However, it seems appropriate to refer the fossils to the Saxifragales and it is believed that the flowers may be close to the source of several modern saxifragalean lines. Among the fossil plant remains from our material another flower with affinity to the Saxifragales has been discovered. It is distinguished from the above described flower in having a bilocular ovary and axile placentation.

The fossil flowers described here represent the oldest epigynous flower known in the fossil record. This report also documents the presence of the Saxifragales in the Cretaceous and demonstrates that the group had already reached a relatively high level of evolution, with syncarpous, inferior and unilocular gynoecia. Although the attainment of the major features of angiosperm diversity within the Cretaceous is suggested by leaf and pollen characters[1,3], this is the first demonstration of these particular advanced floral features within the Cretaceous.

The Saxifragales are represented in the Tertiary by a number of genera and by the end of the Eocene the presence of four families, the Iteaceae, Pittosporaceae, Hydrangeaceae and Saxifragaceae, have been documented by the occurrence of floral structures from the Baltic Amber[21]. Our discovery of saxifragalean flowers in the Cretaceous thus demonstrates that some of the diversity of the group seen in the Lower Tertiary was already evident in the Cretaceous. This is consistent with the central position of the Saxifragales in angiosperm phylogeny postulated by Takhtajan[10] and Hutchinson[11].

We thank Professor W. G. Chaloner of Bedford College, University of London, for helpful suggestions and critical discussion, Professor K. Larsen, University of Aarhus, for helpful discussion, and Höganäs AB for help and material. E.M.F. acknowledges the support of the Danish Natural Science Research Council and the receipt of a British Council Research fellowship.

Received 15 January; accepted 26 March 1981.

1. Doyle, J. A. & Hickey, L. J. in *Origin and Early Evolution of Angiosperms* (ed. Beck, C. B.) 139–206 (Columbia University Press, New York, 1976).
2. Hughes, N. F. *Bot. Rev.* **43**, 105–127 (1977).
3. Hickey, L. J. & Doyle, J. A. *Bot. Rev.* **43**, 3–104 (1977).
4. Beck, C. B. (ed.) *Origin and Early Evolution of Angiosperms*, 1–341 (Columbia University Press, New York, 1976).
5. Kemp, E. M. *Palaeontology* **11**, 421–434 (1968).
6. Wolfe, J. A., Doyle, J. A. & Page, V. M. *Ann. Mo. bot. Gdn* **62**, 801–824 (1975).
7. Knobloch, E. *Sb. geol. Ved, Rada TG* **19**, 79–132 (1977).
8. Dilcher, D. L., Crepet, W. L., Beeker, C. D. & Reynolds, H. C. *Science* **191**, 845–856 (1976).
9. Dilcher, D. L. *Rev. Palaeobot. Palynol.* **27**, 291–328 (1979).
10. Takhtajan, A. L. *Flowering Plants, Origin and Dispersal*, 1–310 (Oliver & Boyd, Edinburgh, 1969).
11. Hutchinson, J. *Evolution and Phylogeny of Flowering Plants*, 1–717 (Academic, London and New York, 1969).
12. Stopes, M. C. & Fujii, K. *Phil. Trans. R. Soc.* B**201**, 1–90 (1910).
13. Tiffney, B. H. *Nature* **265**, 136–137 (1977).
14. Grönwall, K. A. *Sver. geol. Unders. Afh.* C**261**, 1–185 (1915).
15. Lundegren, A. *Geol. För. Stockh. Förh.* **53**, 298–320 (1931).
16. Ross, N. E. *Bull. geol. Instn Univ. Upsala* **34**, 25–43 (1949).
17. Skarby, A. *Acta Univ. Stockh.* **16**, 1–60 (1968).
18. Cope, M. J. & Chaloner, W. G. *Nature* **283**, 647–649 (1980).
19. Scott, A. C. & Collinson, M. E. in *Scanning Electron Microscopy in the Study of Sediments* (ed. Whally, B.) 137–167 (Geo-Abstracts, Norwich, 1978).
20. Alvin, K. L. *Palaeontology* **17**, 587–598 (1974).
21. Conwentz, H. *Die Flora des Bernsteins, 2. Die Angiospermen des Bersteins*, 1–140 (Danzig, 1886).

Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems

K. Sherman*, C. Jones*, L. Sullivan*, W. Smith†, P. Berrien† & L. Ejsymont‡

* National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Narragansett, Rhode Island 02882, USA
† National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Sandy Hook, New Jersey 07732, USA
‡ Morski Instytut Rybacki, Zaklad Sortowania i Oznaczania Planktonu, Szczecin, Poland

It has been suggested, on the basis of model simulations and slowly accumulating empirical data, that changes in the structure of marine ecosystems may be caused as much by changes in the trophic levels as by environmental factors[1,2]. Support for this is found in recently observed shifts in species abundance of North Sea fish stocks, where large catches in the 1970s of small, fast-growing, opportunistic plankton-feeding fishes—sprat, sand eel and Norway pout—have been accounted for as the result of the replacement by these species of depleted herring and mackerel stocks[3,4]. This suggestion is difficult to confirm, as knowledge of the abundance of these 'opportunistic' species since the mid-1960s is largely limited to catch data for the North Sea[5]. The only sand eel report independent of commercial fisheries catch data is for larvae collected in 1948–68, just before the sharp decline in mackerel and herring stocks[6]. The area surveyed did not, however, cover all the major population centres in the North Sea. In support of replacement, we describe here evidence from the north-west Atlantic which indicates that population explosions of small, fast-growing sand eel can coincide with depletions of larger tertiary predators, including herring and mackerel in a continental shelf ecosystem. Sand eels serve as an important link in marine food chains, preying on secondary producers and constituting an important food of higher trophic level fish and marine mammals[7,8].

Our results are based on 6 years (1974–79) of ichthyoplankton surveys, conducted by the United States, Poland and the Soviet Union on the continental shelf off the east coast of the United States, as part of a joint MARMAP study of shelf productivity. [MARMAP is the first multinational programme for measuring long-term changes in key structural components of very large marine ecosystems. At present 260,000 km^2 of the north-west Atlantic continental shelf are being sampled routinely to measure changes in key structural components, including primary production (^{14}C), chlorophyll *a* phaeophytin, nutrients (NO_2, NO_3, SiO_3, NH_4 and PO_4), zooplankton, ichthyoplankton, fish, benthos, seabirds, water-column temperature, salinity and circulation[9].] Between 6 and 12 surveys were done per year. The sampling area covered the continental shelf and included four sub-areas: Gulf of Maine, Georges Bank, southern New England and middle Atlantic Bight (see Fig. 1). Ichthyoplankton were collected at about 180 locations situated 25–35 km apart and during the 6 yr, we sampled ~6.5 million km^2.

The data presented here are based on population densities of sand eel calculated for the annual spawning period in winter, when sand eel larvae, *Ammodytes* spp., are most abundant. Two species, *A. dubius* and *A. americanus*, reportedly occur in the survey area[10]. Their taxonomy remains confused and we are uncertain whether our collections included only one or both. Thus, until the identity of the larvae is clarified, they are classified as *Ammodytes*.

At each sampling location, tows for ichthyoplankton and zooplankton were made through the water column using a paired bongo-type plankton sampler[11] with 60-cm openings and

0028–0836/81/240486—04$01.00

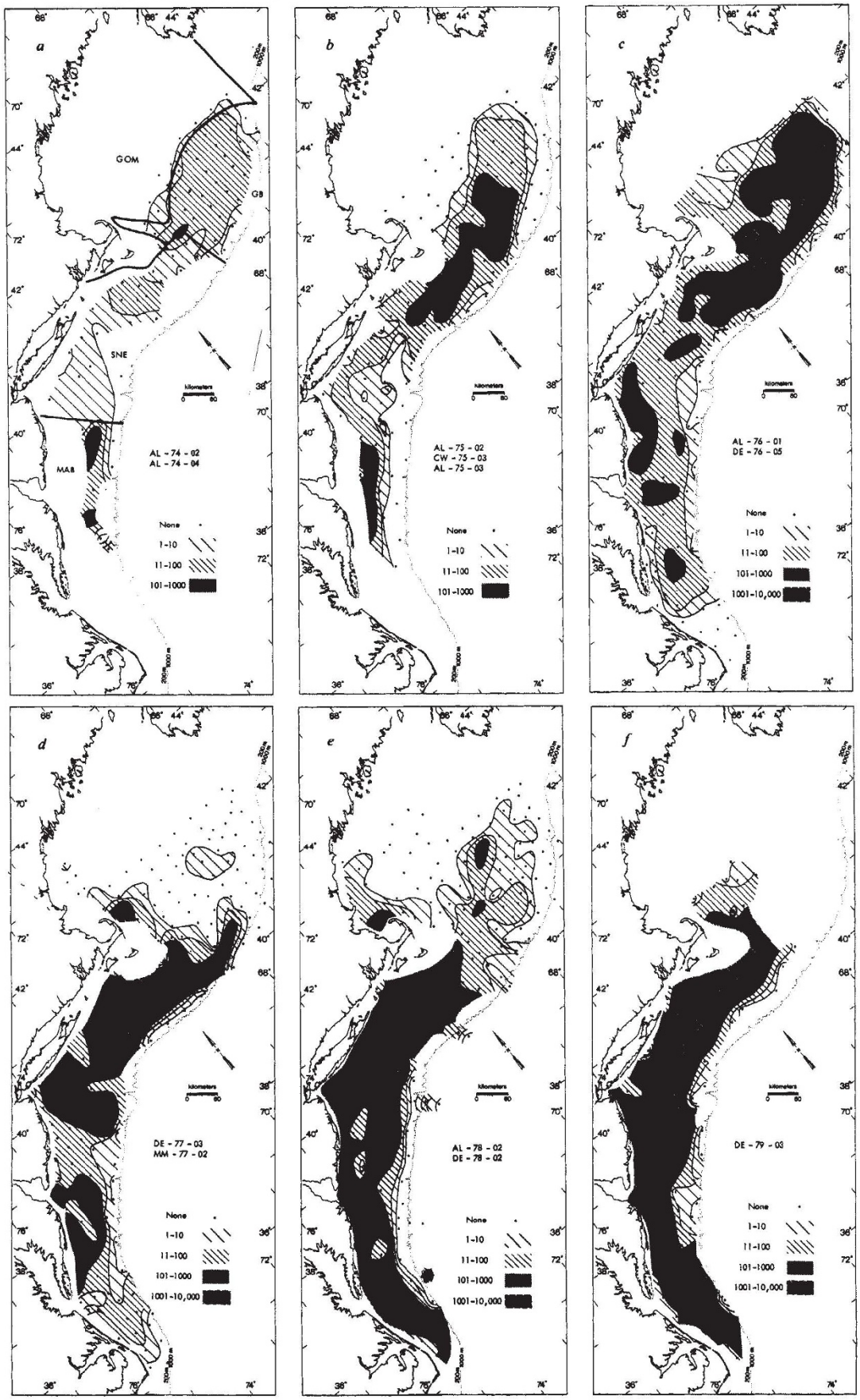


Fig. 1 Increase in abundance of sand eel larvae (*Ammodytes*) on the continental shelf off the north-east United States coast in winter 1974–1979. The four sub-areas of the shelf sampled include the Gulf of Maine (GOM), Georges Bank (GB), southern New England (SNE) and mid-Atlantic Bight (MAB). Samples were collected from the NOAA research vessels: Albatross IV (AL), Delaware II (DE), Commonwealth (CW) and Mount Mitchell (MM). *a*, 11 February–22 March 1974; *b*, 12 February–16 March 1975; *c*, 10 February–24 March 1976; *d*, 12 February–8 April 1977; *e*, 14 February–17 March 1978; *f*, 23 February–15 March 1979. Shading represents number of *Ammodytes* larvae per 10 m^2 surface area.

Table 1 Winter abundance estimates of sand launce, *Ammodytes*, larvae in three sub-areas off northeastern United States

Year		Georges Bank (41,809 km²)	Southern New England (59,906 km²)	Middle Atlantic (58,326 km²)	Total (×10¹⁰)
1974	*k*	33.941	11.216	48.692	
	s.e.	1.054	1.093	1.726	
	Abundance	14.190	6.719	28.400	49.309
	% Of larval fish	55	13	88	
1975	*k*	90.427	51.555	57.044	
	s.e.	1.602	1.220	1.371	
	Abundance	37.806	30.884	33.271	101.961
	% Of larval fish	59	60	90	
1976	*k*	1,018.311	243.798	55.393	
	s.e.	1.990	1.440	1.297	
	Abundance	425.746	146.050	32.309	604.105
	% Of larval fish	97	96	84	
1977	*k*	9.931	603.255	76.991	
	s.e.	1.996	1.446	1.404	
	Abundance	4.152	361.386	44.905	410.443
	% Of larval fish	88	81	71	
1978	*k*	13.916	569.359	313.297	
	s.e.	1.122	1.451	1.332	
	Abundance	5.818	341.080	182.733	529.631
	% Of larval fish	91	92	94	
1979	*k*	442.324	738.239	577.487	
	s.e.	1.934	1.402	1.561	
	Abundance	184.931*	442.250	336.825	964.006
	% Of larval fish	98	79	87	

Abundance estimates were determined by Δ-distribution[25]. Retransformed mean abundance (k) is expressed as larvae per 10 m² surface area. Larval abundance ($\times 10^{10}$) is expansion of k to reflect the sub-area size. (See Berrien *et al.*[26] for discussion of rationale and procedures for use of Δ-distribution.)

* Estimate based on limited sampling.

nets of 0.333 and 0.505 mm mesh. These nets were towed at ship speeds ranging from 1.5 to 3.5 knots. The bongo sampler was lowered obliquely from the surface to within 5 m of the bottom at a wire speed of 50 m min^{-1} and retrieved at 20 m min^{-1}. Water filtered through the net was measured with a flow meter and a time–depth recorder was used to measure the towing path of the sampler. The ichthyoplankton samples were sorted, species identified and enumerated, and measured at the Plankton Sorting Center, Szczecin, Poland. The data on ichthyoplankton were calculated initially as numbers of larvae per 10 m² of sea surface, and expanded to numbers of larvae per km² and numbers of larvae $\times 10^{10}$ for the entire shelf.

The north-west Atlantic ecosystem off the northeastern United States has been subjected to significant fishing stress; fish biomass in the region was reduced by 50% from 1968 to 1975 (ref. 12). Since then, the silver hake and squid stocks have been increasing but herring and mackerel stocks remain low[13]. From 1974 to 1979, coincident with the low mackerel and herring stocks, we observed a population explosion of sand eel larvae increasing from a low shelf density of 49×10^{10} in 1974 to 964×10^{10} in 1979. During this 6-yr period the percentage of sand eel increased from less than 50% of the total mid-winter ichthyoplankton community to more than 85%. A summary of comparisons of abundance levels and percentage composition of sand eel in the ichthyoplankton community among areas and in years is made in Table 1.

The centre of sand eel larval abundance shifted during the years of study. Abundance was low in 1974 and 1975. In 1976 the centre of population density was on Georges Bank. Abundance estimates were significantly lower on Georges Bank in

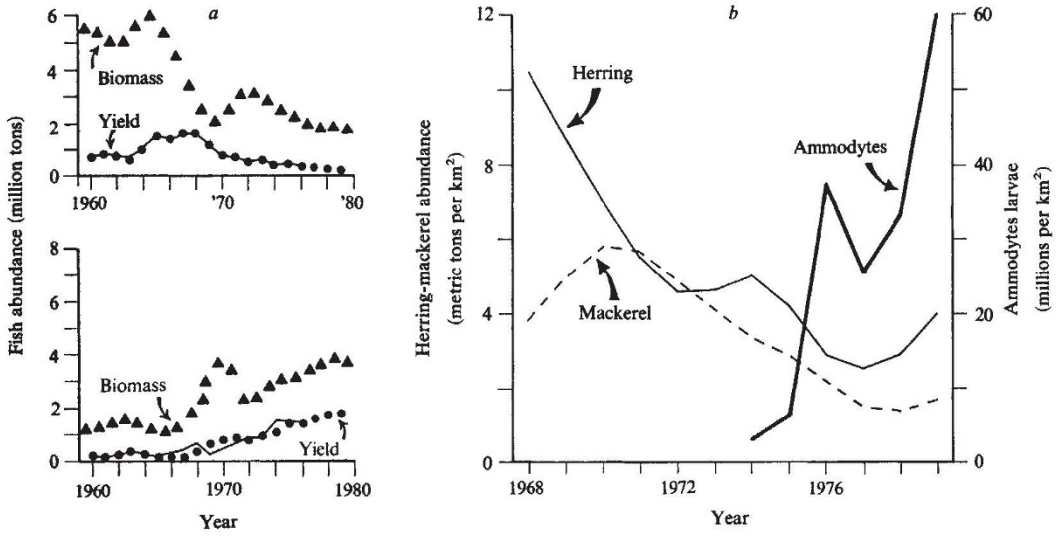


Fig. 2 *a*, Decline in herring and mackerel biomass (▲) and yield (●) (upper graphs), and successive rise in biomass (▲) and yield (●) (lower graphs) of small, fast-growing sprat, sand eels and Norway pout in the North Sea from 1960 to 1979 as depicted by Ursin[3]. *b*, Decline in herring (———) and mackerel (– – –) biomass in metric tons per km² and successive increase in larval *Ammodytes* (———) abundance in millions of larvae per km² for the north-west Atlantic shelf from Cape Hatteras to the Gulf of Maine (1974–1979). Herring densities represent stocks ranging from southern New England to western Nova Scotia and are based on an updating (Waring, personal communication) of the data of Sissenwine and Waring[27]; mackerel densities include stocks ranging from Cape Hatteras to Labrador (1968–1979), based on the data of Anderson[28].

1977 and 1978 but larvea of other taxa were also greatly reduced in number and the percentage contribution of sand eels remained close to 90%. Because of technical difficulties we were unable to complete our early winter survey in 1979. After 1976, the principal centres of abundance were in the southern New England and mid-Atlantic Bight areas; large patches of larvae in densities of over 1,000 per 10 m^2 extending for distances greater than 300 km occurred most frequently off the southern New England coast (Fig. 1).

In the North Sea, the fishery yield for juvenile and adult sand eel, sprat and Norway pout increased from <200,000 metric tons in 1960 to 1.6 million metric tons in 1976. In the absence of a fishery in the north-west Atlantic, it is difficult to estimate the contribution of larval abundance of sand eel to the biomass of adults. Based on available evidence, we conclude that the adult stock is increasing. (1) MARMAP bottom trawl surveys have shown an increasing trend in abundance in southern New England and the mid-Atlantic Bight[14]. (2) An increase in abundance has been observed directly by divers[15], and (3) a significant increase has been observed in the consumption of sand eel by predators from 1968 to 1976 (ref. 16).

The influence of temperature has been suggested as a principal factor in controlling abundance levels of fish stocks on the continental shelves of the north-west Atlantic off the Canadian maritimes and the northeastern United States[17,18]. The reductions in herring and mackerel on both sides of the Atlantic in response to heavy fishing mortality, followed by increases in sand eel and other small, fast-growing fish as shown in Fig. 2*a*, *b* make unlikely the hypothesis that the changes are due to environmental factors. Our findings show that when a large biomass of mid-size predators is removed it can be replaced by smaller, faster-growing, opportunistic species as described for the North Sea[3,4] and observed by us.

The full consequence of structural change with respect to earlier unperturbed status has not yet been documented for large marine ecosystems. We are just starting to obtain the multitrophic level data needed to unscramble inter- and intraspecific ecosystem relationships[9,19–22]. The influence of structural changes on aquatic ecosystems can result in significant economic and aesthetic loss. In a species succession model for the Great Lakes, removal of large predators resulted in the proliferation of fast-growing smaller alewives[23]. A size-component response to structural modification in a large marine ecosystem has been observed in the Antarctic where, based on recent population trends[24], the decrease in the biomass of large blue whales may be in the process of replacement by the faster-growing smaller minke whales and seals. Monitoring of the shelf ecosystem in the north-west Atlantic is continuing in an attempt to measure the impact of any increase in the demersal and pelagic fish-predator field (for example, cod, haddock, hake, mackerel and herring) on the changing structure of the shelf ecosystem.

Received 29 December 1980; accepted 17 March 1981.

1. Steele, J. H. & Frost, B. W. *Phil. Trans. R. Soc.* **B280**, 485–534 (1977).
2. Daan, N. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**, (in the press).
3. Ursin, E. *Cons. int. Explor. Mer C. M. F.* **42** (1977).
4. Andersen, K. P. & Ursin, E. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **172**, 286–291 (1978).
5. Hempel, G. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **172**, 445–449 (1978).
6. Hart, P. J. B. in *The Early Life History of Fish* (ed. Blaxter, J. H. S.) 171–182 (Springer, Berlin, 1974).
7. Bigelow, H. B. & Schroeder, W. C. *Fish. Bull. U.S.A.* **74**, 577 (1954).
8. Reay, P. J. *F. A. O. Fish. Biol. Synopses* **82** (1970).
9. Sherman, K. in *Advanced Concepts on Ocean Measurements for Marine Biology* (eds Diemer, F. P., Vernberg, F. J. & Mirkes, D. Z.) 9–37 (Belle W. Baruch Institute for Marine Biology and Coastal Research, Univ. of S. C. Press, 1980).
10. Richards, S. W., Perlmutter, A. & McAneny, D. C. *Copeia 1963*, 358–377 (1963).
11. Posgay, J. A. & Marak, R. R. *J. Northw. Atl. Fish. Sci.* **1**, 91–99 (1980).
12. Clark, S. H. & Brown, B. E. *Fish. Bull. U.S.A.* **75**, 1–21 (1977).
13. Clark, S. H. & Brown, B. E. *Investigacion pesq.* **43**, 107–122 (1979).
14. Grosslein, M., Langton, R. W. & Sissenwine, M. P. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**, (in the press).
15. Meyer, T. L., Cooper, R. A. & Langton, R. W. *Fish. Bull. U.S.A.* **77**, 243–253 (1979).
16. Bowman, R. *NMFS/NEFC Woods Hole Lab. Ref.* No. 80–05 (1980).
17. Dow, R. L. *J. Cons. int. Explor. Mer* **37**, 274–280 (1977).
18. Sutcliffe, W. H. J., Drinkwater, K. & Muir, B. S. *J. Fish. Res. Bd Can.* **34**, 19–30 (1977).
19. Anderson, K. P. & Ursin, E. *Medd. Dan. Fish.-Havunder. N.S.* **7**, 319–435 (1977).
20. Regier, H. A. & Henderson, H. F. *Trans. Am. Fish. Soc.* **102**, 56–72 (1973).
21. Mills, E. L. & Fournier, R. O. *Mar. Biol.* **54**, 101–108 (1979).
22. Cohen, E., Grosslein, M., Sissenwine, M. & Steime, F. *Cons. int. Explor. Mer C.M.L.* **64** (1980).
23. Smith, S. H. *Bull. Fish. Res. Bd Can.* **25**, 667–693 (1968).
24. Beddington, J. R. & Grenfell, B. T. in *The Management of the Southern Ocean* (eds Mitchell, B. & Sandbrook, R.) 31–40 (International Institute for Environment and Development, London, 1980).
25. Atchinson, J. *J. Am. statist. Ass.* **50**, 272–901 (1955).
26. Berrien, P. L., Naplin, N. A. & Pennington, M. R. in *The Early Life History of Fish II* (eds Lasker, R. & Sherman, K.); *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **178** (in the press).
27. Sissenwine, M. P. & Waring, L. L. *NMFS/NEFC Woods Hole Lab. Ref.* No. 79–12 (1979).
28. Anderson, E. D. *NMFS/NEFC Woods Hole Lab. Ref.* No. 80–29 (1980).

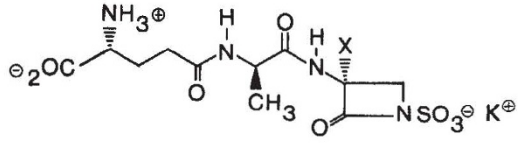
Monocyclic β-lactam antibiotics produced by bacteria

R. B. Sykes, C. M. Cimarusti, D. P. Bonner, K. Bush, D. M. Floyd, N. H. Georgopapadakou, W. H. Koster, W. C. Liu, W. L. Parker, P. A. Principe, M. L. Rathnum, W. A. Slusarchyk, W. H. Trejo & J. S. Wells

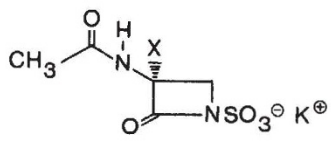
The Squibb Institute for Medical Research, PO Box 4000, Princeton, New Jersey 08540, USA

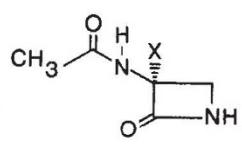
A recent article[1] described two novel monocyclic β-lactam antibiotics produced by bacteria. In the past few years, we have screened bacteria isolated from numerous ecosystems and habitats for their ability to produce β-lactam antibiotics, using a strain of *Bacillus licheniformis* which is specific for molecules containing a β-lactam and which is sensitive down to 100 ng ml^{-1}. From over one million bacterial isolates screened, we have now identified seven related molecules containing β-lactams produced by a range of bacterial species. For this new family of monocyclic β-lactams we suggest the class name 'monobactam'. Bacteria which produce β-lactams are, in reality, relatively common in nature.

The β-lactam most frequently detected in our studies was SQ 26,445 (Fig. 1, I), one of the compounds isolated from a strain of *Pseudomonas acidophila*[1]. β-Lactam-producing strains isolated from 41 separate locations were identified as species of



No.	X
I (SQ 26,445)	OCH_3
II	H





No.	X	No.
III (SQ 26,180)	OCH_3	V
IV	H	VI

Fig. 1 Structures of monobactams I–VI. SQ 26,445 (I) was isolated from a strain of *Gluconobacter*. SQ 26,180 (III) was produced by strains of *Chromobacterium violaceum*.

0028–0836/81/240489—03$01.00