



Sibling Species in the Sea

Nancy Knowlton

Annual Review of Ecology and Systematics, Vol. 24 (1993), 189-216.

Stable URL:

<http://links.jstor.org/sici?sici=0066-4162%281993%2924%3C189%3ASSITS%3E2.0.CO%3B2-F>

Annual Review of Ecology and Systematics is currently published by Annual Reviews.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/annrevs.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact jstor-info@umich.edu.

SIBLING SPECIES IN THE SEA*

Nancy Knowlton

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama or Unit 0948, APO AA 34002-0948

KEY WORDS: marine, invertebrate, taxonomy, cryptic species, speciation

Abstract

Sibling species are common in all major marine groups and habitats. Their abundance reflects both inadequate study of morphological features of living organisms (“pseudo-sibling species”) and divergence in habitat, life history, and chemical recognition systems without parallel divergence in morphology. Many marine sibling species are quite distinct genetically. Others, however, exhibit slight genetic differences whose significance is only clear in sympatry and in combination with other subtle but concordant patterns of differentiation. A large number of abundant, well-studied, or economically important taxa have recently been shown to be complexes of sibling species. The broad habitat and geographic distributions characteristic of many marine species require reevaluation in this context.

INTRODUCTION

Sibling species are species that are difficult or impossible to distinguish based on morphological characters (140). Mayr was the first to broadly review sibling species (138), the existence of which formed a central part of his attack on the morphological species concept (139). There has never been a comprehensive review of sibling species in the sea, and the relevant literature is scattered and sometimes obscure. The taxonomic spectrum is enormous, with thirty-plus phyla of marine invertebrates, in addition to marine vertebrates, angiosperms, algae, fungi, and procaryotes. My primary focus is marine invertebrates, and even here a complete catalogue is not feasible. I exclude from consideration several quasi-marine groups [mangroves, fiddler crabs (see 111), and brine shrimp].

*The US government has the right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.

There is no unambiguous criterion for determining if species are siblings; usage of the term varies considerably across taxonomic groups and authorities. For this review, any species whose distinctiveness has been the source of substantial taxonomic debate or whose discovery was based on non-morphological characters is included under the rubric of sibling species. Thus examples range from species that are readily distinguished morphologically once the appropriate characters are considered ("pseudo-sibling species") to species that are only imperfectly isolated from each other ("semi-species").

PREVALENCE OF MARINE SIBLING SPECIES

Marine sibling species are ubiquitous. They appear to be common in a variety of marine invertebrates (Table 1); marine vertebrates (23, 54, 79, 121, 135, 142, 149, 189, 193, 194, 198, 249) and plants (11, 21, 87, 120, 130, 146, 160, 171) also have numerous examples. They are found from the poles to the tropics, in most known habitats, at depths ranging from intertidal to abyssal. Why are they so common?

Inadequate Information

Our ignorance of the basic biology of most marine species contributes in several ways to the abundance of sibling species. First, methods of preservation for marine organisms destroy many characters taken for granted in other groups. Soft tissues (often including feeding structures) are lost in many marine invertebrates with hard skeletons, as is color in the many soft bodied groups for which liquid preservative is required. This problem is exacerbated by the fact that marine species are less accessible for observation in their natural habitat than are terrestrial species. Second, standard experimental protocols for analysis of the relative importance of genetic and environmental sources of morphological variability (41) are logistically more difficult in the sea, and in the absence of information to the contrary, considerable intraspecific variability is considered "normal." Finally, in many groups of marine organisms, wide geographic ranges have been uncritically accepted as the natural consequence of potentially broad oceanic dispersal. Although a panmictic oceanic soup should make geographic isolation, and thereby speciation less likely (161, 225), the actual frequency of successful long-distance dispersal is largely unknown.

Some groups are especially problematic, for example, sponges generally (22, 196) and those taxa lacking features traditionally employed in sister groups (22, 42, 215). Similarly, poorly known regions such as the deep sea are likely to have many sibling species (72). Even shallow subtidal regions have been routinely visited by scientists only since the 1960s, and the expeditionary style of most tropical taxonomic research is not conducive to the recognition of sibling species.

Table 1 Examples of pseudo-sibling, sibling and semi-species in marine invertebrates.

Taxa	Evidence for differences between species										References	
	Geography ^a	Proteins ^b	mtDNA ^c	Morph ^d	Color ^e	Habitat ^f	Life History ^g	Reproductive isolation ^h				
Porifera												
<i>Clathria</i>	S	distinct	—	slight	—	—	—	—	—	—	—	97
<i>Oscarella</i>	S	1.39	—	yes	yes	dpth,hab	—	—	—	—	—	22
<i>Clathrina</i>	T	1.25–2.06	—	slight	yes	—	—	—	—	—	—	197
<i>Asinella</i>	S	0.36	—	slight	—	—	—	—	—	—	—	202
	S	2.08	—	yes	—	—	—	—	—	—	—	202
<i>Corticium</i>	S	0.79	—	yes	—	hab	—	—	—	—	—	196
<i>Suberites</i>	S	0.02	—	slight	yes	sub	—	—	—	—	—	199
	S	0.41	—	yes	yes	—	lh	—	—	—	—	199
	S	distinct	—	yes	yes	—	—	—	—	—	—	48
<i>Halisarca</i>	S	—	—	slight	—	dpth,sal	lh	—	—	—	—	42
<i>Tethya</i>	S	1.69	—	yes	yes	temp,sal, exp,dpth	lh	—	—	—	—	181, 182
	P	0.27	—	slight	—	—	—	—	—	—	—	182
Cnidaria												
<i>Aglaophenia</i>	S	1.71	—	yes	—	temp	—	—	—	—	—	217
<i>Hydractinia</i>	S	—	1.6	slight	—	temp,dpth,host	—	—	—	—	—	36, 50
	S	distinct	10.8–11.6	slight	—	hab, sal, host	—	—	—	—	—	36, 50
	P	—	4.4	—	—	host	—	—	—	—	—	50
	T	—	1.8	slight	—	host	—	—	—	—	—	36, 50
<i>Sarsia</i>	S	—	—	slight	—	—	lh	—	—	—	—	150
<i>Urticina</i>	S	0.17	—	yes	yes	—	—	—	—	—	—	201
<i>Bunodosoma</i>	S	1.67	—	slight	yes	—	—	—	—	—	—	141
<i>Sagarita</i>	S	0.36	—	yes,sz	yes	sal	lh	—	—	—	—	190
<i>Epitactis</i>	S	—	—	sz	yes	exp,food	lh,beh	—	—	—	—	65

Table 1 (Continued)

Evidence for differences between species									
Taxa	Geography ^a	Proteins ^b	mtDNA ^c	Morph ^d	Color ^e	Habitat ^f	Life History ^g	Reproductive isolation ^h	References
<i>Metridium</i>	S	1.31-1.84	—	yes, sz	yes	exp	lh	—	28, 29, 64
	S	0.82	—	yes, sz	yes	dpth	lh	—	28, 29, 64
	I	0.20	—	slight	—	—	—	—	29, 64
<i>Actinia</i>	T	1.06	—	slight	—	—	—	—	27, 64
	S	0.32	—	slight, sz	yes	temp, dpth	lh	—	39
	S	0.09	—	yes	yes	dpth, exp	lh, beh	—	89
	S	0.10	—	—	yes	—	—	—	200
	T	0.36	—	—	—	—	—	—	8
<i>Montastraea</i>	S	0.06-0.26	—	yes	yes	dpth	lh, beh	—	114, 230, 231
<i>Acropora</i>	S	distinct	—	slight	yes	exp, dpth	lh	asyn	9, 115
<i>Stylophora</i>	S	—	—	yes	—	dpth	phys	—	74
<i>Pocillopora</i>	S	distinct	—	yes	yes	exp	—	asyn	176, 208
<i>Agaricia</i>	T	—	—	yes	—	dpth	—	asyn	176
<i>Nemertea</i>	T	—	—	yes	—	dpth	lh, beh	—	76, 174
<i>Lineus</i>	S	—	—	yes	yes	dpth, sub	lh	asyn	154, 228
<i>Oerstedtia</i>	S	>1.00	—	slight	yes	—	lh, beh	—	77, 246
<i>Polychaeta</i>	S	2.83	—	slight	yes	dpth, sub	—	—	211, 212
<i>Axiothella</i>	P	—	—	slight, sz	—	food	lh, beh	—	251
<i>Abarenicola</i>	S	—	—	slight, sz	yes	dpth, sub	beh	asyn	90
<i>Spirobranchus</i>	S	—	—	yes	—	dpth, sub	lh, beh	inc	134
<i>Pomatocerus</i>	S	0.83	—	slight	yes	dpth	—	—	59
<i>Microphthalmus</i>	T	—	—	yes, sz	yes	—	lh, beh	asyn	243
<i>Capitella</i>	P	—	—	yes, sz	yes	—	—	—	243
	S, P, T, I	>1.00	—	slight, sz	—	dpth, sal, time	lh	inc, chr	80-83

<i>Nereis</i>	I	—	—	sz	—	—	—	—	phys	inc,chr	240
	P	—	—	—	—	—	—	—	—	inc,chr?	240
<i>Platynereis</i>	T, I	—	—	slight,sz	—	—	—	sal	lh	inc	195
<i>Nerine</i>	S, T	—	—	—	—	—	—	—	lh	inc	167, 195
<i>Polydora</i>	S	—	—	slight,sz	—	—	—	dpth	—	—	14
	S	<0.01-0.50	—	slight	—	—	—	sub	phys, lh	inc	173
	P	—	—	slight,sz	—	—	—	sub, dpth	lh	inc	172
<i>Boccardia</i>	S	—	—	yes	—	—	yes	—	beh	—	169
<i>Sireblospio</i>	I	—	—	—	—	—	yes	sub	lh	asyn	55
	P	—	—	yes	—	—	—	—	—	inc	172
<i>Malacoceros</i>	S, P, I	—	—	—	—	—	—	—	—	—	126
	S	distinct	—	slight	—	—	yes	exp, hab	lh	inc	86
<i>Ophryotrocha</i>	P	distinct	—	—	—	—	yes	—	—	inc	86
<i>Pholoe</i>	S, P, T, I	distinct	—	slight	—	—	—	—	lh	inc,chr	4, 177
<i>Ophelia</i>	S	—	—	slight,sz	—	—	—	dpth	lh	asyn	45
<i>Chaetozone</i>	S	distinct	—	slight	—	—	—	dpth	—	—	24
	S	—	—	slight	—	—	yes	sub	—	asyn, inc?	46
<i>Tharyx</i>	S	—	—	yes	—	—	yes	dpth	lh	—	46
<i>Australonuphis</i>	P	—	—	—	—	—	—	—	lh	asyn	75
<i>Mollusca</i>	S	distinct	—	slight,sz	—	—	yes	dpth, exp	lh	—	166
<i>Mytilus</i>	P	0.16-0.28	3.0-4.0	slight,sz	—	—	yes	exp, dpth,	lh	asyn, inc	73, 187, 223
								sal, temp			
<i>Mercenaria</i>	S, P	distinct	—	slight	—	—	yes	sal, dpth, temp	phys	asyn	55a, 56
<i>Macoma</i>	P	0.25-1.80	—	slight,sz	—	—	yes	sal, temp	—	—	18, 147, 224
	T	0.18	—	—	—	—	yes	—	—	—	18, 224
<i>Cardium</i>	S	distinct	—	slight	—	—	—	sub, sal, dpth	beh, phys	inc	25, 26, 109
	P	distinct	—	—	—	—	—	—	—	—	25, 26
<i>Saccostrea</i>	S	0.19	—	—	—	—	—	—	—	—	33
<i>Crassostrea</i>	P	0.17-0.45	—	yes, sz	—	—	yes	temp, hab	—	chr, asyn	3, 33

Table 1 (Continued)

Taxa	Evidence for differences between species										References
	Geography ^a	Proteins ^b	mtDNA ^c	Morph ^d	Color ^e	Habitat ^f	Life History ^g	Reproductive isolation ^h			
<i>Littorina</i>	S	0.48	—	slight,sz	yes	sal,sub	—	—	155, 168		
	S	0.04–0.07	—	slight	yes	hab	lh	inc	236, 237, 238a		
	S	0.28–0.47	—	slight,sz	yes	dpth,temp	lh	—	12, 20, 105		
<i>Collisella</i>	S	0.35	—	slight,sz	yes	temp	lh	—	44, 157, 236		
	S	distinct	—	slight	yes	temp, dpth	—	—	156		
<i>Conus</i>	S	—	—	yes	yes	—	—	—	40		
<i>Amalida</i>	P	distinct	—	yes	—	—	—	—	148		
<i>Oxysteles</i>	S	0.58	—	slight	yes	dpth	—	—	92a		
<i>Cuthona</i>	P	—	—	slight	yes	—	lh	—	94		
<i>Doto</i>	S	0.63	—	slight,sz	yes	food	lh	—	122, 153		
<i>Hanleya</i>	S	—	—	sz	—	food,sub,dpth	lh	—	238		
<i>Nototodarus</i>	P	distinct	—	slight	yes	temp	—	—	192		
<i>Nautilus</i>	S, P	0.12–0.21	—	yes,sz	yes	—	—	—	235, 252		
Arthropoda											
<i>Endeis</i>	S	1.42	—	slight,sz	—	dpth	—	—	108		
<i>Acartia</i>	S	1.01	—	slight,sz	yes	hab	—	—	143		
	I	—	—	slight,sz	—	—	lh	inc	38		
<i>Calanus</i>	S, P, I	distinct	—	slight,sz	—	temp,dpth	—	asyn,chr	69, 132		
<i>Pseudocalanus</i>	S, P, I	distinct	—	slight,sz	—	hab,temp, dpth,time	lh,phys	chr	70, 144, 145, 188		
<i>Tisbe</i>	S, T	0.24–>1.00	—	slight	—	sal,food, sub,exp	beh	inc,chr	13, 86, 133, 186, 226, 234		
<i>Doridicola</i>	S	—	—	—	yes	host	beh	—	129		
<i>Balanus</i>	I	0.21	—	—	—	—	—	—	68		

<i>Chthamalus</i>	S, P	0.46-0.75	—	slight	—	—	—	91
	S	distinct	—	slight	sal,exp,dpth	—	—	53, 204
	P	distinct	—	slight	—	—	—	52, 53
	S, P	distinct	—	slight	exp.sal,temp	—	—	51
<i>Jaera</i>	S, T	0.11-0.45	—	slight	sal,dpth, sub,exp	—	pref.inc,chr	203
	P	0.58	—	—	—	—	—	165
<i>Cyathura</i>	S	0.16	—	slight	sal,temp	—	inc	32, 191
<i>Gammarus</i>	P	0.46	—	slight	temp	—	inc	32, 191
<i>Eogammarus</i>	S	distinct	—	sz	sub,dpth	lh	pref,asyn	205, 206
<i>Penaeus</i>	S	distinct	9.6	slight	dpth,sub	—	—	62, 162
<i>Periclimenes</i>	S	—	—	slight	host,food	beh	—	159
<i>Alpheus</i>	S	0.11-0.22	7.6-16.4	slight	host,dpth	—	inc	111, 113
	I	0.03-0.27	6.6-19.2	slight	—	—	inc	113
<i>Panopeus</i>	S	0.003	—	slight	sal,hab, dpth,food	beh	asyn	210, 220, 244
	P	distinct	—	slight	—	—	—	210, 244
<i>Menippe</i>	P	0.11	—	slight	hab,sal	lh,beh,phys	—	16, 17, 245
<i>Trapedia</i>	S	0.22-0.42	—	slight	—	—	—	99, 100
	T	0.17	—	—	—	—	—	100
Bryozoa								
<i>Alcyonidium</i>	S	0.87	—	yes,sz	—	—	—	214
	S	0.56	—	slight?	sub,hab,dpth	—	—	215, 216
	S	distinct	—	yes	—	—	—	215, 216
	P	distinct	—	slight	—	—	—	215, 216
<i>Stylopoma</i>	S	0.34-1.11	—	slight	—	—	—	102
Echinodermata								
<i>Thyonella</i>	S	distinct	—	yes	sub	phys,beh	—	131
<i>Acanthaster</i>	S	0.20	—	yes	hab,food,dpth	—	inc	158
	T	0.05	—	yes	—	—	—	158

Table 1 (Continued)

Taxa	Evidence for differences between species							References	
	Geography ^a	Proteins ^b	mtDNA ^c	Morph ^d	Color ^e	Habitat ^f	Life History ^g		Reproductive isolation ^h
<i>Echinaster</i>	S	0.03	—	yes,sz	yes	dpth,hab	lh	asyn	183, 221
<i>Asterias</i>	S	0.40	—	yes	yes	dpth,temp	—	—	185
<i>Asterina</i>	S	—	—	yes	—	—	lh	—	2
<i>Leptasterias</i>	S	>1.00	—	slight,sz	yes	dpth,exp	lh,beh,phys	—	31, 60, 61
<i>Ophiotoma</i>	S	0.19	—	yes,sz	yes	—	—	—	117
<i>Ophiactis</i>	S	0.66	—	yes,sz	—	—	lh	—	152
<i>Diadema</i>	I	>1.00	—	sz	—	sub	lh	—	151, 152
<i>Echinometra</i>	I	0.04	5.3	—	—	—	—	asyn	15, 123, 124
	I	0.34	6.0	slight	—	—	—	inc	15, 123, 125
	S	0.12–0.26	1.0–3.0	slight	yes	hab,sub,exp	beh	chr,inc	136, 163, 218, 219, 222
Asciacea									
<i>Botryllus</i>	S	0.91	—	yes,sz	yes	—	—	—	5
<i>Corella</i>	S	—	—	yes	—	dpth,exp	lh	asyn	118

^aS-sympatric, P-parapatric, T-transoceanic, I-interoceanic (see text for details)

^bNet's distances for protein electrophoresis where given; otherwise differences are indicated by "distinct". Note that exact distance formulations and loci examined are not the same across studies.

^cpercent sequence divergence

^dyes-species clearly distinct in morphology, slight-differences in morphology are subtle, sz-species differ in size

^eyes-species can be distinguished by color or color pattern

^fhab-habitat, sub-substrata, dpth-depth or tidal range, exp-exposure to water movement, sal-salinity, temp-temperature, time-seasonal differences

^glh-life history, beh-behavior, phys-physiology

^hinc-reproductive incompatibility (mating, fertilization or development), pref-preference for conspecific mating, asyn-asynchronous reproductive cycles, chr-chromosomal or DNA quantity differences. Reproductive isolation may be partial or complete.

Nevertheless, what is most perturbing about the species complexes discovered to date is that so many of them are abundant, accessible, or economically important (see below), often with a long history of continuous study. Only in the 1980s have the species complexes in European periwinkles been clarified (168, 236), and persistent controversy surrounds the taxonomy of the edible European mussel (187). Thus, we are probably seeing the tip of the iceberg in more poorly known groups and environments. Only in rare taxa are complexes of sibling species a priori less likely; for members of these groups, the probability of finding a mate is already low.

Biological Characteristics

Marine sibling species are not only artifacts of ignorance. Decoupling of morphological and ecological divergence inevitably leads to sibling species. Potential competitors with simple body plans may coexist due to differences unrelated to morphology; the highly divergent symbiotic dinoflagellates (zooxanthellae) (179), once thought to be a single species, are a particularly good example. This phenomenon is not limited to morphologically simple forms, however; coexistence of various sessile taxa may be due primarily to differences in dispersal abilities and settlement preferences of their larvae (see below).

The dominant role of chemical recognition systems in the sea is perhaps the biggest obstacle to recognizing species boundaries, because our ability to analyze this sensory modality is so limited relative to auditory and visual systems, and because, unlike visual systems, there are few if any morphological correlates. The difference even extends to marine angiosperms that, unlike many of their terrestrial relatives, lack visually oriented pollinators. The role of narrowly tuned chemical recognition systems in the settlement preferences of larvae (153, 154), in the choice of mates (69, 111, 205, 240), and in egg-sperm recognition (161) has been implicated or suggested for a number of sibling species complexes. Chemically mediated recognition may also be more highly correlated with greater host specificity (63), compared to visual recognition. The possibility that the narrow "bandwidths" characteristic of many chemoreceptors (1) might facilitate divergence deserves further consideration.

PATTERNS OF DIVERGENCE

Morphology

The fact that sibling species are defined on the basis of their morphological similarity might lead one to assume that all sibling species are difficult to distinguish on these grounds. Many past taxonomic uncertainties, however,

stem from failure to use or consider potentially available characters. In corals, for example, colony growth form has been underutilized as a taxonomic character because of the false assumption that growth form is invariably highly plastic (74, 114) and because large colonies are generally collected as small fragments (9). Taxa that are conspicuously distinct when alive, or when considered in their entirety, are better termed pseudo-sibling species. They make up a substantial proportion of the examples listed in Table 1.

Even sibling species in the narrow sense often have minor morphological differences that are only noticed once species are recognized for other reasons. In some cases these differences are subtle but diagnostic. In others a discriminant function analysis can reliably separate most or all members of sibling species complexes when morphological characters individually show considerable overlap. The most sophisticated analyses of subtle morphological distinctions have involved modular organisms, in which intracolony measurements can be used to partially factor out nongenetic variability (41, 103). Diagnostic characters are obviously easier to use, but why some characters tend to be diagnostic and others not is unclear. Color pattern differences in decapods are often diagnostic (111), perhaps because they conspicuously reflect minor developmental shifts affecting the migration of pigment-bearing cells. Differences in pattern may, in general, be more discrete than measurements or counts, which often require statistical analyses. Extensive asexual reproduction may also be associated with smaller differences and greater overlap between species (30).

Reproductive Isolation

For the many taxa that reproduce sexually and do not engage in widespread hybridization, the biological species concept remains central to the recognition of sibling species. Actual tests of reproductive isolation in marine taxa are relatively few, however. Table 1 includes several examples of the two main categories of prezygotic isolation: behavioral incompatibility (111, 203, 240) and lack of synchronicity in reproductive activity. Fertilization barriers (e.g. 36, 125, 134) and postzygotic developmental failures (e.g. 36, 109, 234) are also known. Studies of F₂s are more limited due to difficulties in rearing marine organisms to sexual maturity; most work has been done on taxa with direct development and short generation times (e.g. 4, 203, 206). Chromosomal differences are also used as indirect indicators of reproductive incompatibility (Table 1).

Taxa that are exclusively clonal or widely hybridizing pose the biggest problems for the biological species concept, and definitions based on demographic exchangeability have been proposed for such cases (213). Obligately asexual species are rare in the sea; the clearest example of morphologically similar but ecologically distinct clones is found in the bivalve *Lasaea* (101). Maintenance of morphological integrity despite widespread

hybridization has been suggested as the reason behind the fuzzy species boundaries in corals (175, 248) and in a group of reef fishes (67).

Genetics

Many marine sibling species have major genetic differences (e.g. values of Nei's genetic distance of 0.5 or greater, Table 1). This pattern is consistent with Mayr's (139) prediction, although pseudo-sibling species should be discounted in this context. There are, however, a growing number of examples that show very little genetic differentiation (e.g. Nei's genetic distance of 0.1 or less, Table 1). Because such cases are intrinsically more difficult to identify, it is hard to estimate their actual importance.

Species that are genetically very similar but morphologically distinctive are not sibling species in the traditional sense (although etymologically the term should apply). They are, however, of special interest because of their implications for punctuated morphological evolution. The morphologically distinct European and American lobsters, with a Nei's genetic distance of only 0.11 (92), are one of the few known examples among marine invertebrates.

Ecology

Sympatric sibling species, when examined carefully, are often found to exhibit distinct habitat preferences defined by depth, salinity, or exposure, or preferences within an area for particular substrata or hosts (Table 1). The extraordinarily broad habitat ranges characteristic of many marine "species" need to be reexamined in this light. Successional differences between sibling species, reflecting temporal partitioning of resources in response to seasonal change or disturbance, are also documented (80). For allopatric sibling species, ecological divergence is less important, and only reproductive divergence may occur.

Divergence in life history is the most conspicuous difference between many sibling species (Table 1), and alleged intraspecific variation in larval biology (poecilogony) has been shown to be an artifact of unrecognized sibling species in many other cases (95). These differences may represent equally successful, alternative life history solutions to a given environmental regime; alternatively, slight differences in habitat may select for marked life history changes, particularly across sharp disturbance gradients in the intertidal and shallow subtidal (112).

PATTERNS OF PROXIMITY

Sympatry, allopatry, and parapatry are traditionally defined on the basis of whether individuals are "within cruising range" of each other, but the distinctions between these categories are not always clear (71). This is particularly true in the sea for several reasons. Patterns of dispersal are very

hard to document directly, and inference from characteristics of larvae and adults is not always straightforward (34). The algal symbiont-supplied larva of the coral *Pocillopora damicornis* has been interpreted both as an agent of trans-Pacific transport (175) and as a means to permit rapid growth following dispersal of a few centimeters (207). For many species, routine short-distance dispersal may be punctuated by much rarer, very long distance events, leading to complex hierarchical patterns of connections between populations (112).

Because of these uncertainties, and because different taxa have such different dispersal capabilities, I use loose, primarily biogeographic definitions of these terms. Thus the "sympatric" taxa of Table 1 are those for which at least modest contact via larval or adult dispersal is conceivable, even though the species may show distinct habitat preferences on scales ranging from coarse (depth, exposure, salinity) to fine (different hosts or settlement sites within an area). "Parapatric" taxa are those with largely nonoverlapping distributions along a continuous coastline, even though the nature or even the existence of a zone of contact is not established in many cases. The geographic scale of parapatry may be very fine in species with limited dispersal potential (251). "Allopatric" distributions may be transoceanic (east versus west or north versus south) or interoceanic. Whether such distributions are actually disjunct is discussed below. Distributions limited to particular islands or island groups within an ocean are also in a gray zone between parapatry and allopatry, depending on the dispersal abilities of the taxa considered.

Sibling species with at least partially overlapping ranges make up over half of the examples cited in Table 1, undoubtedly because species boundaries are most clearly documented in sympatry (140). For the same reason, sibling species with small degrees of genetic divergence are almost exclusively sympatric. The latter is not necessarily misleading, however, since allopatric forms may show greater genetic divergence by the time they achieve reproductive incompatibility than do sympatric forms (49).

Parapatrically distributed, slightly differentiated forms of well-known taxa are responsible for some of the most vexing taxonomic controversies in the sea. These taxa also include the few well-documented cases of marine hybrid zones (the bivalves *Mytilus*, *Mercenaria*, and *Macoma*, and the crab *Menippe*, Table 1). One of the most intensively documented is that between two *Mytilus* species (223). Although hybrid zones are broader in the sea than on land, analysis of this case suggests that the zone is in fact quite narrow, considering the potential dispersal ability of larval mussels. Other genetic discontinuities along coastlines may also mark the existence of sibling species, particularly when several independent characters show the same pattern (e.g. 250).

The nature of transoceanic and interoceanic relationships clearly depends on the dispersal abilities of the taxa being considered. Some species, for example, are regularly carted around the world by humans (37) and are

genuinely cosmopolitan as a consequence. Large, widely ranging marine vertebrates also show limited genetic discontinuities across or between oceans (10, 84). However, species with more limited dispersal abilities, whether by swimming, larval drift, or rafting (93, 96, 184, 227), show considerable variability in the extent of genetic connection between spatially separated populations.

Spatially isolated tropical taxa are often separated by great distances, and the rise of the Isthmus of Panama approximately 3–3.5 million years ago severed all connections between the tropical Atlantic and Pacific. Taxa separated by this barrier show substantial reproductive isolation (113, 124, 125), and some Atlantic and Pacific tropical taxa apparently diverged long before the land barrier was complete (113, 160). Lower divergence within than between oceans suggests that long-distance dispersal occurs at least occasionally (116, 178), and consequently the taxonomic significance of modest transoceanic divergence is often unclear (158).

Cold-water populations divided along an east-west axis are separated by smaller distances than are tropical taxa. Moreover, there is no antarctic land barrier between the oceans, and the arctic land barrier between the Pacific and Atlantic disappeared for nonabyssal taxa with the opening of the Bering Strait approximately 3.5 million years ago (232). Thus many more cold-water than tropical taxa have ranges spanning both coasts of a single ocean or the Pacific and the Atlantic (21). Divergence can be quite small between (164) and across (11, 78) oceans for cold-water taxa, although more marked but taxonomically ambiguous divergence does occur in some cases (7, 27).

Antitropical distributions are well known in a variety of groups (127, 233). Gene flow across the equator is currently restricted not only by distance but by the requirement of passage through either warm or cold but deep water. Vermeij (233) argued that antitropical populations of marine invertebrates in the Atlantic were last connected over three million years ago; extrapolation from trans-isthmian studies (see above) suggests that most such cognate taxa have achieved reproductive isolation. Connections between some antitropical taxa appear to be considerably more recent, however [e.g. in the eastern Pacific (127) and for algae generally (229, 233)].

IMPLICATIONS

Systematics

Defining species boundaries is the primary problem raised by sibling species, and several conclusions emerge from the examples discussed above. First, search for a single, universally applicable character, apart from unequivocal demonstration of reproductive isolation, is counterproductive. Any single

difference, be it a locus or a spine, is open to question, because differences clearly associated with species boundaries in some situations represent intraspecific polymorphisms in others (e.g. 27). Thus, in the absence of clear-cut barriers to reproduction, the most compelling evidence for species boundaries is the existence of concordant suites of unrelated morphological, behavioral, physiological, or genetic characters (6, 119, 187, 247). Such evidence is particularly persuasive when the same patterns differentiating taxa can be documented in more than one site, as has been shown for the species complexes in *Mytilus* (187) and *Montastraea* (114, 231). In cases where the character set is more limited, extrapolating from other representatives of the group is possible but potentially misleading, as even a single genus may exhibit a diverse array of patterns (e.g. 13). The possibility of selection for reproductive divergence in sympatry makes extrapolation from sympatric to allopatric examples particularly difficult.

Many methods used to test for sibling species, like protein electrophoresis or discriminant function analysis, profit from or require the a priori recognition of groups whose distinctiveness can be subsequently tested. Cluster analysis of preserved material may be used to define groups, particularly in modular taxa (41, 103). Nevertheless, sibling species are often easier to distinguish when alive (111, 119, 122), making two weeks in the field worth two years in the laboratory during the initial phases of investigation. Subsequent morphological analyses cannot be neglected if nonliving or fossil material is to be identified, however, and may be essential for nomenclatural reasons.

Many sibling species complexes present nomenclatural nightmares, because various forms were correctly recognized by earlier workers and subsequently synonymized. Even when only a single name exists, unambiguous assignment of older type specimens to one of many sympatric forms may be difficult unless the morphological differences subsequently recognized are relatively clearcut.

As sibling species continue to be recognized, many genera are going to increase substantially in size; the genus *Tisbe*, for example, has climbed from a few to over 63 species (133). The temptation to split a genus simply on the basis of its size should be resisted, however, because this has no philosophical justification and hinders subsequent retrieval of information (140). Informal species groups, or subgenera where appropriate phylogenetic analyses support them, are the preferred solution for genera that may ultimately contain hundreds or even thousands of species.

Finally, it is generally assumed that species-level taxonomy and higher level phylogeny are decoupled. At the generic level, however, the degree of splitting can have an important influence on the branching patterns and the reliability of the analysis (103).

Speciation

Evaluation of the relative importance of various modes of speciation in the sea (225) is obviously hampered by uncertainty as to what constitutes a species. Not only are the basic biogeographic patterns obscured by our ignorance, but topics such as the evolutionary importance of phenotypic plasticity (242) are impossible to evaluate when species are poorly defined. The complexity of dispersal in the sea poses several additional obstacles to understanding. For example, ignorance of actual dispersal distances makes documentation of sympatric speciation much more difficult. The potential for larval dispersal or swimming or rafting of adults facilitates remixing of species that originated allopatrically to a greater extent than in terrestrial or freshwater groups, so that reconstructions of past distributions are more difficult. Nevertheless, a few general comments can be made, particularly for those sibling species where genetic evidence suggests relatively recent origins.

One of the clearest examples of the classic or “dumbbell” model of allopatric speciation is the evolution of reproductive incompatibility between numerous tropical eastern Pacific and Caribbean taxa separated by the rise of the Isthmus of Panama 3.0 to 3.5 million years ago (113, 124, 125). This model system has two important limitations, however. First, oceanographic differences between the two oceans are extreme, so that the effects of selection and genetic drift cannot be readily distinguished. Second, it is difficult to generalize from this example of an impenetrable barrier to situations where sporadic immigration occurs.

Very occasional arrivals of small founder populations to isolated islands could result in speciation via founder effects. Compatible with this scenario is the substantial (and probably underestimated) endemism at the species level in the Galapagos (104) and Hawaiian (98, 106, 107) archipelagoes. The best direct evidence of this process for a marine invertebrate is the rapid development of reproductive isolation in a laboratory culture of a polychaete (239). Substantial genetic divergence has also been documented for a small founding population of littorine snails (110), but the reproductive biology of this population has not been examined. Many of the sibling species complexes in Table 1 have larvae with limited dispersal ability and sedentary or sessile adults with the potential for occasional rafting. This suite of characters should facilitate founder-event speciation followed by subsequent reestablishment of sympatry.

Other, more controversial modes of speciation should also be considered. The large number of sibling species complexes with different depth distributions could reflect clinal speciation (225); even within the intertidal and shallow subtidal, gradients in selection pressures might be steep enough to

override the effects of dispersal for sessile or sedentary taxa with direct development. The same process might operate on a broader latitudinal scale for taxa with planktonic larvae, particularly where current patterns or salinity gradients partially disrupt gene flow. Marine species with narrow host or substratum specificities recall suggested examples of sympatric speciation on land (57, 58, 206). Speciation in hosts and symbionts may (50) or may not (179) be coupled.

The role of sexual selection in driving divergence of reproductive recognition systems (241) is receiving growing attention for marine organisms. The process may occur via interacting adults (111, 205, 240) or gametes (150, 161). In both cases recognition systems are subjected to the opposing pressures of sexual selectivity versus finding a mate. One might expect recognition systems at the gamete level to be somewhat less narrowly tuned, because short-lived sperm and eggs in sea water have fewer alternatives than do longer-lived adults. Molecular diversity of the proteins governing egg-sperm interactions is surprisingly high, however, and may play an important role in speciation of marine invertebrates with the potential for regular long-distance dispersal (161). Sexual selection may also promote increasing host specificity (47) when mating occurs on the host (e.g. 57, 58).

Ecology

The abundance of sibling species in the sea has ecological as well as evolutionary implications. Perhaps most obvious is the impact of sibling species on global marine biodiversity (137), although the magnitude of the effect is difficult to estimate. For example, the polychaete *Chaetozone setosa* is described as cosmopolitan with a depth distribution ranging from the intertidal to 4436 m, but a single study of three sites spanning 65 km (two intertidal and one at 80 m) indicated that each had a distinct species (46). The increase in diversity from discoveries of sibling species is often four-fold or greater in comprehensive studies of a single region (e.g. *Hydractinia*, *Actinia*, *Ophryotrocha*, *Capitella*, *Macoma*, *Doto*, *Calanus*, *Chthamalus*, *Tisbe*, *Jaera*, *Panopeus*, *Stylopoma*, *Echinometra*). As a very rough estimate, one can expect the number of marine species to increase by an order of magnitude if sibling species are considered.

Many of the theoretical issues that have dominated ecology for several decades—such as competition—depend on a clear understanding of species. The examples reviewed above indicate that species are more specialized and more geographically circumscribed in the sea than has been appreciated previously. Thus, lottery models of competitively equivalent species (43) are potentially less relevant than classical competition theory in explaining the coexistence of species, and the evolution of highly specialized, locally appropriate competitive mechanisms (e.g. 35) is conceivable. Moreover, the

prevalence of life history divergence between sibling species suggests that disturbance is better viewed as a resource for which competition occurs (85), rather than as an agent disrupting competitive interactions (the more traditional marine perspective).

Nor can field ecologists overlook these taxonomic “details,” because growing evidence suggests that competitors and predators are not blind to the differences among the sibling species with which they interact. Scattered throughout the literature are references to differences among sibling species in their competitive abilities (89, 114, 133, 174, 210) and relationships with symbionts and predators (2, 22, 73, 89, 152, 181, 192).

Indicator, Managed, and Model Species

Failure to recognize sibling species results in bad science, both basic and applied. For example, at least three marine taxa widely used as indicators of environmental quality have been found to consist of several sibling species whose differences have important implications for their use in bioassays (83, 114, 128). Sibling species have been discovered in a number of fisheries (e.g. *Crassostrea*, *Nototodarus*, *Penaeus*, *Menippe* in Table 1; see also 121, 135, 166, 193, 194, 198), with obvious implications for management. Conservation measures currently being developed for marine environments can also be jeopardized by failure to recognize sibling species (19). Finally, many of the taxa listed in Table 1 have been used as model systems for basic biological investigations where mixtures of unrecognized sibling species could seriously confound interpretations of results.

There is another, more positive side to this coin, however. Species complexes provide ideal and largely untapped grist for the mill of comparative biology. The considerable variation in reproductive biology exhibited within species complexes provides a perfect framework for testing theories on life history evolution (112), and there are many other possible applications. Suites of sibling species should be viewed as nature’s gift of replicated, well-controlled variation, rather than as a taxonomic nuisance.

CONCLUSIONS: ORNITHOLOGY FOR THE COPEPODOLOGIST

In the preceding review I have argued that sibling species are rife in marine environments, and that failure to recognize them cripples evolutionary and ecological understanding of the sea. In contrast, Mayr (139) estimates that only 5% of birds are sibling species. I conclude by offering a marine transmogrification of ornithological research for those readers who remain unconvinced of the significance of this difference.

Consider a world where birds are only occasionally seen alive by the handul

of scientists who study their alpha taxonomy. They arrive in museums either as colorless corpses in jars of Formalin, or as skeletal material alone. The bills are often delicate structures whose normal shape cannot be reliably inferred from preserved material. Growth is often indeterminate, and weather can affect both the size and shape of the skeleton. Field observations are generally limited to a few hours a day, and identification keys, where they exist, generally lack information on color pattern and bill shape. Communication between individuals probably occurs via pheromones, as there are few auditory or visual displays. Contact chemicals or micrometeorological conditions appear to shape preferences for nesting and feeding sites.

Under such circumstances would we even know of Darwin's finches or MacArthur's warblers? Probably not, with obvious implications for our understanding of the natural world. Not only marine research suffers, however. Comparisons between marine, terrestrial, and freshwater environments (88, 112, 161, 209, 225) illuminate the workings of ecological and evolutionary processes generally. Are fish like birds, corals like plants, and shrimp like insects, and if so why? The answers will elude us until we know what the fish, corals, and shrimp really are.

ACKNOWLEDGMENTS

I thank E. Bermingham, N. Boury-Esnault, L. Buss, B. Coull, E. Duffy, D. Fautin, L. Hillis, J. Jackson, E. Mayr, D. Morse, J. Olsen, S. Palumbi, G. Paulay, A. Solé-Cava, J. Thorpe, and J. Weinberg for sharing their ideas, manuscripts and references, J. Jackson for his comments and support, and F. Bouche, J. Jara and the staff of the Smithsonian libraries for getting the relevant literature onto my desk. Over the years the National Science Foundation and the Smithsonian Institution have generously supported my research on sibling species of shrimps and corals.

Literature Cited

1. Ache BW. 1988. Integration of chemosensory information in aquatic invertebrates. In *Sensory Biology of Aquatic Animals*, ed. J Atema, RR Fay, AN Popper, WN Tavolga, pp. 387-401. New York: Springer-Verlag
2. Aчитув Y. 1969. Studies on the reproduction and distribution of *Asterina burtoni* Gray and *A. wega* Perrier (Asteroidea) in the Red Sea and the eastern Mediterranean. *Israel J. Zool.* 18:329-42
3. Ahmed M. 1975. Speciation in living oysters. *Adv. Mar. Biol.* 13:357-97
4. Åkesson B. 1984. Speciation in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *Fortsch. Zool.* 29:299-316
5. Aron S, Solé-Cava A. 1991. Genetic evaluation of the taxonomic status of two varieties of the cosmopolitan ascidian *Botryllus niger* (Asciaceae: Botryllidae). *Biochem. Syst. Ecol.* 19: 271-76
6. Avise JC, Ball RM Jr. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. In *Oxford Surveys in Evolutionary Biology*, ed. D Futuyma, J Antonovics, 7:45-67. Oxford: Oxford Univ. Press
7. Avise JC, Helfman GS, Saunders NC, Hales LS. 1986. Mitochondrial DNA

- differentiation in North Atlantic eels: population genetic consequences of an unusual life history pattern. *Proc. Natl. Acad. Sci. USA* 83:4350–54
8. Ayre DJ. 1990. Population subdivision in Australian temperate marine invertebrates: larval connections versus historical factors. *Aust. J. Ecol.* 15:403–11
 9. Ayre DJ, Veron JEN, Dufty SL. 1991. The corals *Acropora palifera* and *Acropora cuneata* are genetically and ecologically distinct. *Coral Reefs* 10: 13–18
 10. Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidis J, O'Brien SJ. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344:238–40
 11. Bakker FT, Olsen JL, Stam WT, van den Hoek C. 1992. Nuclear ribosomal DNA internal transcribed spacer regions (ITS1 and ITS2) define discrete biogeographic groups in *Cladophora albida* (Chlorophyta). *J. Phycol.* 28: 839–45
 12. Bandel K, Kadolsky D. 1982. Western Atlantic species of *Nodilittorina* (Gastropoda: Prosobranchia): comparative morphology and its functional, ecological, phylogenetic and taxonomic implications. *Veliger* 25:1–42
 13. Battaglia B, Volkmann-Rocco B. 1973. Geographic and reproductive isolation in the marine harpacticoid copepod *Tisbe*. *Mar. Biol.* 19:156–60
 14. Bellan G, LaGardère F. 1971. *Nerine mesnili*, n. sp., spionidien méconnu des plages sableuses de la province Lusitanienne. *Bull. Soc. Zool. France* 96:571–79 (Suppl.)
 15. Bermingham E, Lessios HA. 1993. Rate variation of protein and mtDNA evolution as revealed by sea urchins separated by the Isthmus of Panama. *Proc. Natl. Acad. Sci. USA*. 90:2734–38
 16. Bert TM. 1986. Speciation in western Atlantic stone crabs (genus *Menippe*): the role of geological processes and climatic events in the formation and distribution of species. *Mar. Biol.* 93: 157–70
 17. Bert TM, Harrison RG. 1988. Hybridization in western Atlantic stone crabs (genus *Menippe*): evolutionary history and ecological context influence species interactions. *Evolution* 42:528–44
 18. Beukema JJ, Meehan BW. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Mar. Biol.* 90:27–33
 19. Bickham JW. 1983. Sibling species. In *Genetics and Conservation*, ed. CM Schonewald-Cox, SM Chambers, B MacBryde, L Thomas, pp. 96–106. Menlo Park, Calif: Benjamin/Cummings
 20. Borkowski TV. 1974. Growth, mortality, and productivity of south Floridian Littorinidae (Gastropoda: Prosobranchia). *Bull. Mar. Sci.* 24:409–38
 21. Bot PVM, Stam WT, Boele-Bos SA, van den Hoek C, van Delden W. 1989. Biogeographic and phylogenetic studies in three North Atlantic species of *Cladophora* (Cladophorales, Chlorophyta) using DNA-DNA hybridization. *Phycologia* 28:159–68
 22. Boury-Esnault N, Solé-Cava AM, Thorpe JP. 1992. Genetic and cytological divergence between colour morphs of the Mediterranean sponge *Oscarella lobularis* Schmidt (Porifera, Demospongiae, Oscarellidae). *J. Nat. Hist.* 26:271–84
 23. Bowen BW, Meylan AB, Avise JC. 1991. Evolutionary distinctiveness of the endangered Kemp's ridley sea turtle. *Nature* 352:709–11
 24. Britton-Davidian J, Amoureux L. 1982. Biochemical systematics of two sibling species of polychaete annelids: *Ophelia bicornis* and *O. radiata*. *Biochem. Syst. Ecol.* 10:351–54
 25. Brock V. 1979. Habitat selection of two congeneric bivalves, *Cardium edule* and *C. glaucum* in sympatric and allopatric populations. *Mar. Biol.* 54: 149–56
 26. Brock V. 1987. Genetic relations between the bivalves *Cardium (Cerastoderma) edule*, *Cardium lamarcki* and *Cardium glaucum*, studied by means of crossed immunoelectrophoresis. *Mar. Biol.* 93:493–98
 27. Bucklin A. 1985. Biochemical genetic variation, growth and regeneration of the sea anemone, *Metridium*, of British shores. *J. Mar. Biol. Assoc. UK* 65: 141–57
 28. Bucklin A. 1987. Growth and asexual reproduction of the sea anemone *Metridium*: comparative laboratory studies of three species. *J. Exp. Mar. Biol. Ecol.* 110:41–52
 29. Bucklin A, Hedgcock D. 1982. Biochemical genetic evidence for a third species of *Metridium* (Coelenterata: Actiniaria). *Mar. Biol.* 66:1–7
 30. Budd AF. 1990. Longterm patterns of morphological variation within and among species of reef-corals and their relationship to sexual reproduction. *Syst. Bot.* 15:150–65
 31. Bullimore B, Crump RG. 1982. En-

- zyme electrophoresis and taxonomy of two species of *Asterina* (Asteroidea). In *Echinoderms: Proceedings of the International Conference, Tampa Bay*, ed. JM Lawrence, pp. 185–88. Rotterdam: A.A. Balkema
32. Bulnheim H-P, Scholl A. 1981. Genetic variation between geographic populations of the amphipods *Gammarus zaddachi* and *G. salinus*. *Mar. Biol.* 64:105–15
 33. Buroker NE, Hershberger WK, Chew KK. 1979. Population genetics of the family Ostreidae. II. Interspecific studies of the genera *Crassostrea* and *Saccostrea*. *Mar. Biol.* 54:171–84
 34. Burton RS. 1983. Protein polymorphisms and genetic differentiation of marine invertebrate populations. *Mar. Biol. Lett.* 4:193–206
 35. Buss LW, Jackson JBC. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* 113:223–34
 36. Buss LW, Yund PO. 1989. A sibling species group of *Hydractinia* in the north-eastern United States. *J. Mar. Biol. Assoc. UK* 69:857–74
 37. Carlton JT. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanogr. Mar. Biol. Ann. Rev.* 23: 313–71
 38. Carrillo B-G E, Miller CB, Wiebe PH. 1974. Failure of interbreeding between Atlantic and Pacific populations of the marine calanoid copepod *Acartia clausi* Giesbrecht. *Limnol. Oceanogr.* 19:452–58
 39. Carter MA, Thorpe JP. 1981. Reproductive, genetic and ecological evidence that *Actinia equina* var. *mesembryanthemum* and var. *fragacea* are not conspecific. *J. Mar. Biol. Assoc. UK* 61:79–93
 40. Chaney HW. 1987. A comparative study of two similar Panamic cones: *Conus ximenes* and *Conus mahogani*. *Veliger* 29:428–36
 41. Cheetham AH, Jackson JBC, Hayek LC. 1993. Quantitative genetics of bryozoan phenotypic evolution. 1. Rate tests for random change versus selection in differentiation of living species. *Evolution*. In press
 42. Chen W-T. 1976. Reproduction and speciation in *Halisarca*. In *Aspects of Sponge Biology*, ed. FW Harrison, RR Cowden, pp. 113–32. New York: Academic
 43. Chesson P. 1991. A need for niches? *TREE* 6:26–28
 44. Chow V. 1987. Morphological classification of sibling species of *Littorina* (Gastropoda: Prosobranchia): discretionary use of discriminant analysis. *Veliger* 29:359–66
 45. Christie G. 1982. The reproductive cycles of two species of *Pholoe* (Polychaeta: Sigalionidae) off the Northumberland coast. *Sarsia* 67:283–92
 46. Christie G. 1985. A comparative study of the reproductive cycles of three Northumberland populations of *Chaetozone setosa* (Polychaeta: Cirratulidae). *J. Mar. Biol. Assoc. UK* 65:239–54
 47. Colwell RK. 1986. Population structure and sexual selection for host fidelity in the speciation of hummingbird flower mites. In *Evolutionary Processes and Theory*, ed. S Karlin, E Nevo, pp. 475–95. Orlando, FL: Academic
 48. Connes R, Diaz J-P, Nègre G, Paris J. 1974. Étude morphologique, cytologique et sérologique de deux formes de *Suberites massa* de l'étang de Thau. *Vie Milieu* 24:213–24
 49. Coyne JA, Orr HA. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43: 362–81
 50. Cunningham CW, Buss LW, Anderson C. 1991. Molecular and geologic evidence of shared history between hermit crabs and the symbiotic genus *Hydractinia*. *Evolution* 45:1301–16
 51. Dando PR, Southward AJ. 1980. A new species of *Chthamalus* (Crustacea: Cirripedia) characterized by enzyme electrophoresis and shell morphology: with a revision of other species of *Chthamalus* from the western shores of the Atlantic Ocean. *J. Mar. Biol. Assoc. UK* 60:787–831
 52. Dando PR, Southward AJ. 1981. Existence of “Atlantic” and “Mediterranean” forms of *Chthamalus montagui* (Crustacea, Cirripedia) in the western Mediterranean. *Mar. Biol. Lett.* 2:239–48
 53. Dando PR, Southward AJ, Crisp DJ. 1979. Enzyme variation in *Chthamalus stellatus* and *Chthamalus Montagui* (Crustacea: Cirripedia): evidence for the presence of *C. montagui* in the Adriatic. *J. Mar. Biol. Assoc. UK* 59:307–20
 54. Davies JL. 1963. The antitropical factor in cetacean speciation. *Evolution* 17: 107–16
 55. Dean D, Blake JA. 1966. Life-history of *Boccardia hamata* (Webster) on the east and west coasts of North America. *Biol. Bull.* 130:316–30
 - 55a. Dillon RT Jr. 1992. Minimal hybrid-

- ization between populations of the hard clams, *Mercenaria mercenaria* and *Mercenaria campechiensis*, co-occurring in South Carolina. *Bull. Mar. Sci.* 50:411-16
56. Dillon RT Jr, Manzi JJ. 1989. Genetics and shell morphology in a hybrid zone between the hard clams *Mercenaria mercenaria* and *M. campechiensis*. *Mar. Biol.* 100:217-22
 57. Duffy JE. 1992. Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. *Mar. Ecol. Prog. Ser.* 90:127-38
 58. Duffy JE. 1993. Genetic population structure in two tropical sponge-dwelling shrimps that differ in dispersal potential. *Mar. Biol.* In press
 59. Ekaratne K, Burfitt AH, Flowerdew MW, Crisp DJ. 1982. Separation of the two Atlantic species of *Pomatoceros*, *P. lamarckii* and *P. triquetrum* (Annelida: Serpulidae) by means of biochemical genetics. *Mar. Biol.* 71:257-64
 60. Emson RH, Crump RG. 1979. Description of a new species of *Asterina* (Asteroidea), with an account of its ecology. *J. Mar. Biol. Assoc. UK* 59:77-94
 61. Emson RH, Crump RG. 1984. Comparative studies on the ecology of *Asterina gibbosa* and *A. phylactica* at Lough Ine. *J. Mar. Biol. Assoc. UK* 64:35-53
 62. Fast AW., Lester LJ, ed. 1992. *Marine Shrimp Culture: Principles and Practices*. Amsterdam: Elsevier
 63. Fautin DG. 1991. The anemonefish symbiosis: what is known and what is not. *Symbiosis* 10:23-46
 64. Fautin DG, Bucklin A, Hand C. 1989. Systematics of sea anemones belonging to genus *Metridium* (Coelenterata: Actiniaria), with a description of *M. giganteum* new species. *Wasmann J. Biol.* 47:77-85
 65. Fautin DG, Chia F-S. 1986. Revision of sea anemone genus *Epiactis* (Coelenterata: Actiniaria) on the Pacific coast of North America, with descriptions of two new brooding species. *Can. J. Zool.* 64:1665-74
 66. Fava G, Volkmann B. 1975. *Tisbe* (Copepoda: Harpacticoida) species from the lagoon of Venice. 1. Seasonal fluctuations and ecology. *Mar. Biol.* 30:151-65
 67. Fischer EA. 1980. Speciation in the hamlets (*Hypoplectrus*: Serranidae)—a continuing enigma. *Copeia* 1980:649-59
 68. Flowerdew MW. 1983. The circum-boreal barnacle *Balanus balanoides* (L.) and its subpopulations. In *Protein Polymorphism: Adaptive and Taxonomic Significance*, ed. GS Oxford, D Rollinson, pp. 75-84. London: Academic
 69. Frost BW. 1974. *Calanus marshallae*, a new species of calanoid copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. *Mar. Biol.* 26:77-99
 70. Frost BW. 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can. J. Zool.* 67:525-51
 71. Futuyama DJ, Mayer GC. 1980. Non-allopatric speciation in animals. *Syst. Zool.* 29:254-71
 72. Gage JD, Tyler PA. 1991. *Deep-Sea Biology*. Cambridge: Cambridge Univ. Press
 73. Gardner JPA. 1992. *Mytilus galloprovincialis* (Lmk) (Bivalvia, Mollusca): the taxonomic status of the Mediterranean mussel. *Ophelia* 35:219-43
 74. Gattuso J-P, Pichon M, Jaubert J. 1991. Physiology and taxonomy of scleractinian corals: a case study in the genus *Stylophora*. *Coral Reefs* 9: 173-82
 75. Gibbs PE. 1971. A comparative study of reproductive cycles in four polychaete species belonging to the family Cirratulidae. *J. Mar. Biol. Assoc. UK* 51:745-69
 76. Glynn PW, Gassman NJ, Eakin CM, Cortes J, Smith DB, Guzman HM. 1991. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). 1. Pocilloporidae. *Mar. Biol.* 109:355-68
 77. Gontcharoff M. 1959. Rearing of certain nemertean (genus *Lineus*). *Ann. N.Y. Acad. Sci.* 77:93-95
 78. Grant WS. 1984. Biochemical population genetics of Atlantic herring, *Clupea harengus*. *Copeia* 1984:357-64
 79. Grant WS. 1987. Genetic divergence between congeneric Atlantic and Pacific Ocean fishes. In *Population Genetics and Fishery Management*, ed. N Ryman, F Utter, pp. 225-46. Seattle: Univ. Wash. Press
 80. Grassle JF, Grassle JP. 1977. Temporal adaptations in sibling species of *Capitella*. In *Ecology of Marine Benthos*, ed. BC Coull, pp. 177-89. Columbia, SC: Univ. South Carolina Press
 81. Grassle JP. 1980. Polychaete sibling species. In *Aquatic Oligochaete Biology*, ed. RO Brinkhurst, DG Cook, pp. 25-32. New York: Plenum
 82. Grassle JP, Gelfman CE, Mills SW.

1987. Karyotypes of *Capitella* sibling species, and of several species in the related genera *Capitellides* and *Capitomastus* (Polychaeta). *Biol. Soc. Wash. Bull.* 7:77-88
83. Grassle JP, Grassle JF. 1976. Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science* 192: 567-69
84. Graves JE, Ferris SD, Dizon AE. 1984. Close genetic similarity of Atlantic and Pacific skipjack tuna (*Katsuwonus pelamis*) demonstrated with restriction endonuclease analysis of mitochondrial DNA. *Mar. Biol.* 79:315-19
85. Grubb PJ. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52:107-45
86. Guérin J-P, Kerambrun P. 1984. Role of reproductive characters in the taxonomy of spionids and elements of speciation in the "*Malacoceros fuliginosus* complex". *Fortsch. Zool.* 29:317-33
87. Guiry MD, West JA. 1983. Life history and hybridization studies on *Gigartina stellata* and *Petrocelis cruenta* (Rhodophyta) in the North Atlantic. *J. Phycol.* 19:474-94
88. Hay ME, Fenical W. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. *Annu. Rev. Ecol. Syst.* 19:111-45
89. Haylor GS, Thorpe JP, Carter MA. 1984. Genetic and ecological differentiation between sympatric colour morphs of the common intertidal sea anemone *Actinia equina*. *Mar. Ecol. Prog. Ser.* 16:281-89
90. Healy EA, Wells GP. 1959. Three new lugworms (Arenicolidae, Polychaeta) from the north Pacific area. *Proc. Zool. Soc. Lond.* 133:315-35 + 4 pl.
91. Hedgecock D. 1979. Biochemical genetic variation and evidence of speciation in *Chthamalus* barnacles of the tropical eastern Pacific Ocean. *Mar. Biol.* 54:207-14
92. Hedgecock D, Nelson K, Simons J, Shleser R. 1977. Genic similarity of American and European species of the lobster *Homarus*. *Biol. Bull.* 152:41-50
- 92a. Heller J, Dempster Y. 1991. Detection of two coexisting species of *Oxysteles* (Gastropoda: Trochidae) by morphological and electrophoretic analyses. *J. Zool. Lond.* 223:395-418
93. Highsmith RC. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Mar. Ecol. Prog. Ser.* 25:169-79
94. Hirano YJ, Hirano YM. 1991. Poecilogony or cryptic species? Two geographically different development patterns observed in "*Cuthona pupillae* (Baba, 1961)" (Nudibranchia: Aeolidoidea). *J. Molluscan Stud.* 57:133-41
95. Hoagland KE, Robertson R. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy. *Biol. Bull.* 174:109-25
96. Hoffmann AJ. 1987. The arrival of seaweed propagules at the shore: a review. *Bot. Mar.* 30:151-65
97. Hooper JNA, Capon RJ, Keenan CP, Parry DL. 1991. Morphometric and biochemical differences between sympatric populations of the *Clathria* "spicata" species complex (Demospongiae: Poecilosclerida: Microcionidae) from northern Australia. See Ref. 170, pp. 271-88
98. Hourigan TF, Reese ES. 1987. Mid-ocean isolation and the evolution of Hawaiian reef fishes. *TREE* 2: 187-91
99. Huber ME. 1985. Allometric growth of the carapace in *Trapezia* (Brachyura, Xanthidae). *J. Crust. Biol.* 5:79-83
100. Huber ME. 1985. Population genetics of eight species of *Trapezia* (Brachyura: Xanthidae), symbionts of corals. *Mar. Biol.* 85:23-36
101. Hughes RN. 1989. *A Functional Biology of Clonal Animals*. London: Chapman & Hall
102. Jackson JBC, Cheetham AH. 1990. Evolutionary significance of morpho-species: a test with cheilostome Bryozoa. *Science* 248:579-83
103. Jackson JBC, Cheetham AH. 1993. Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. Pres. 15th Ann. Spring Systematics Symp., Field Mus. Nat. Hist. Chicago. In press
104. James MJ, ed. 1991. *Galápagos Marine Invertebrates*. New York: Plenum
105. Janson K. 1985. Genetic variation in three species of Caribbean periwinkles, *Littorina angustior*, *L. lineolata*, and *L. ziczac* (Gastropoda: Prosobranchia). *Bull. Mar. Sci.* 37:871-79
106. Jokiel PL. 1987. Ecology, biogeography and evolution of corals in Hawaii. *TREE* 2:179-82
107. Kay EA, Palumbi SR. 1987. Endemism and evolution of Hawaiian marine invertebrates. *TREE* 2:183-86
108. King PE, Thorpe JP, Wallis GP. 1986. A biochemical genetic and morphological investigation of the species within the genus *Endeis* Philippe (Pycno-

- gonida: Endeidae) in Britain. *J. Exp. Mar. Biol. Ecol.* 98:115–28
109. Kingston P. 1973. Interspecific hybridization in *Cardium*. *Nature* 243:360
 110. Knight AJ, Hughes RN, Ward RD. 1987. A striking example of the founder effect in the mollusc *Littorina saxatilis*. *Biol. J. Linnean Soc.* 32:417–26
 111. Knowlton N. 1986. Cryptic and sibling species among the decapod Crustacea. *J. Crust. Biol.* 6:356–63
 112. Knowlton N, Jackson JBC. 1993. Inbreeding and outbreeding in marine invertebrates. In *The Natural History of Inbreeding and Outbreeding*, ed. NW Thornhill, pp. 200–49. Chicago: Univ. Chicago Press
 113. Knowlton N, Weigt LA, Solórzano LA, Mills DK, Bermingham E. 1993. Divergence in proteins, mitochondrial DNA and reproductive compatibility across the Isthmus of Panama. *Science*. 260:1629–32
 114. Knowlton N, Weil E, Weigt LA, Guzmán HM. 1992. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. *Science* 255:330–33
 115. Kojis BL. 1986. Sexual reproduction in *Acropora* (*Isopora*) species (Coelenterata: Scleractinia). *Mar. Biol.* 91:291–309
 116. Kooistra WHCF, Stam WT, Olsen JL, van den Hoek C. 1992. Biogeography of *Cladophoropsis membranacea* (Chlorophyta) based on comparisons of nuclear rDNA ITS sequences. *J. Phycol.* 28:660–68
 117. Kwast KE, Foltz DW, Stickle WB. 1990. Population genetics and systematics of the *Leptasterias hexactis* (Echinodermata: Asteroidea) species complex. *Mar. Biol.* 105:477–89
 118. Lambert G, Lambert CC, Abbott DP. 1981. *Corella* species in the American Pacific northwest: distinction of *C. inflata* Huntsman, 1912 from *C. willmeriana* Herdman, 1898 (Ascidacea, Phlebobranchia). *Can. J. Zool.* 59:1493–504
 119. Lang JC. 1984. Whatever works: the variable importance of skeletal and of non-skeletal characters in scleractinian taxonomy. *Palaeontol. Am.* 54:18–44
 120. Larkum AWD, McComb AJ, Shepherd SA. 1989. *Biology of Seagrasses*. Amsterdam: Elsevier
 121. Lavery S, Shaklee JB. 1991. Genetic evidence for separation of two sharks, *Carcharhinus limbatus* and *C. tilstoni*, from northern Australia. *Mar. Biol.* 108:1–4
 122. Lemche H. 1976. New British species of *Doto* Oken, 1815 (Mollusca: Opisthobranchia). *J. Mar. Biol. Assoc. UK* 56:691–706
 123. Lessios HA. 1981. Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the Isthmus of Panama. *Evolution* 35:618–34
 124. Lessios HA. 1984. Possible prezygotic reproductive isolation in sea urchins separated by the Isthmus of Panama. *Evolution* 38:1144–48
 125. Lessios HA, Cunningham CW. 1990. Gametic incompatibility between species of the sea urchin *Echinometra* on the two sides of the Isthmus of Panama. *Evolution* 44:933–41
 126. Levin LA. 1984. Multiple patterns of development in *Streblospio benedicti* Webster (Sponiidae) from three coasts of North America. *Biol. Bull.* 166:494–508
 127. Lindberg DR. 1991. Marine biotic interchange between the northern and southern hemispheres. *Paleobiology* 17: 308–24
 128. Lobel PB, Belkhole SP, Jackson SE, Lonerich HP. 1990. Recent taxonomic discoveries concerning the mussel *Mytilus*: implications for biomonitoring. *Arch. Environ. Contam. Toxicol.* 19:508–12
 129. Lønning S, Vader W. 1984. Sibling species of *Doridicola* (Copepoda: Lichomolgidae) from California sea anemones: biology and host specificity. *J. Exp. Mar. Biol. Ecol.* 77:99–135
 130. Maggs CA, Douglas SE, Fenety J, Bird CJ. 1992. A molecular and morphological analysis of the *Gymnogongrus devoniensis* (Rhodophyta) complex in the North Atlantic. *J. Phycol.* 28:214–32
 131. Manwell C, Baker CMA. 1963. A sibling species of sea cucumber discovered by starch gel electrophoresis. *Comp. Biochem. Physiol.* 10:39–53
 132. Manwell C, Baker CMA, Ashton PA, Corner EDS. 1967. Biochemical differences between *Calanus finmarchicus* and *C. helgolandicus*. *Mar. Biol. Assoc. UK* 47:145–69
 133. Marcotte BM. 1984. Behaviourally defined ecological resources and speciation in *Tisbe* (Copepoda: Harpacticoida). *J. Crust. Biol.* 4:404–16
 134. Marsden JR. 1992. Reproductive isolation in two forms of the serpulid polychaete, *Spirobranchus polycerus* (Schmarda) in Barbados. *Bull. Mar. Sci.* 51:14–18
 135. Masuda Y, Takeoka S, Tabeta O, Dotsu Y. 1987. Genetic differences

- between two newly described swell-fishes of the genus *Lagocephalus* from southern Kyushu, Japan. *Nippon Suisan Gakkaishi* 53:767-72
136. Matsuoka N, Hatanaka T. 1991. Molecular evidence for the existence of four sibling species within the sea-urchin, *Echinometra mathaei* in Japanese waters and their evolutionary relationships. *Zool. Sci.* 8:121-33
 137. May RM. 1992. Bottoms up for the oceans. *Nature* 57:78-79
 138. Mayr E. 1948. The bearing of the new systematics on genetical problems. The nature of species. *Adv. Genet.* 2:205-37
 139. Mayr E. 1963. *Animal Species and Evolution*. Cambridge: Harvard Univ. Press
 140. Mayr E, Ashlock PD. 1991. *Principles of Systematic Zoology*. New York: McGraw-Hill. 2nd ed.
 141. McCommas SA, Lester LJ. 1980. Electrophoretic evaluation of the taxonomic status of two species of sea anemone. *Biochem. Syst. Ecol.* 8:289-92
 142. McDonald MA, Smith MH, Smith MW, Novak JM, Johns PE, DeVries AL. 1992. Biochemical systematics of notothenioid fishes from Antarctica. *Biochem. Syst. Ecol.* 20:233-41
 143. McKinnon AD, Kimmerer WJ, Benzie JAH. 1992. Sympatric sibling species within the genus *Acartia* (Copepoda: Calanoida): a case study from Westernport and Port Phillip Bays, Australia. *J. Crust. Biol.* 12:239-59
 144. McLaren IA, Laberge E, Corkett CJ, Sévigny J-M. 1989. Life cycles of four species of *Pseudocalanus* in Nova Scotia. *Can. J. Zool.* 67:552-58
 145. McLaren IA, Sévigny J-M, Frost BW. 1989. Evolutionary and ecological significance of genome sizes in the copepod genus *Pseudocalanus*. *Can. J. Zool.* 67:565-69
 146. Medlin LK. 1991. Morphological and genetic variation within the diatom *Skeletonema costatum* (Bacillariophyta): evidence for a new species, *Skeletonema pseudocostatum*. *J. Phycol.* 27:514-24
 147. Meehan BW. 1985. Genetic comparison of *Macoma balthica* (Bivalvia, Telinidae) from the eastern and western North Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 22:69-76
 148. Michaux B. 1987. An analysis of allozymic characters of four species of New Zealand *Amalda* (Gastropoda: Olividae: Ancillinae) *NZ J. Zool.* 14: 359-66
 149. Miller PJ, El-Tawil MY. 1974. A multidisciplinary approach to a new species of *Gobius* (Teleostei: Gobiidea) from southern Cornwall. *J. Zool. Lond.* 174:539-74
 150. Miller RL. 1982. Identification of sibling species within the "*Sarsia tubulosa* complex" at Friday Harbor, Washington (Hydrozoa: Anthomedusae). *J. Exp. Mar. Biol. Ecol.* 62:153-72
 151. Mladenov PV, Emson RH. 1988. Density, size structure and reproductive characteristics of fissiparous brittle stars in algae and sponges: evidence for interpopulational variation in levels of sexual and asexual reproduction. *Mar. Ecol. Prog. Ser.* 42:181-94
 152. Mladenov PV, Emson RH. 1990. Genetic structure of populations of two closely related brittle stars with contrasting sexual and asexual life histories, with observations on the genetic structure of a second asexual species. *Mar. Biol.* 104:265-74
 153. Morrow CC, Thorpe JP, Picton BE. 1992. Genetic divergence and cryptic speciation in two morphs of the common subtidal nudibranch *Doto coronata* (Opisthobranchia: Dendronotacea: Dotoidae) from the northern Irish Sea. *Mar. Ecol. Prog. Ser.* 84:53-61
 154. Morse DE, Hooker N, Morse ANC, Jensen RA. 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J. Exp. Mar. Biol. Ecol.* 116:193-217
 155. Moyse J, Thorpe JP, Al-Hamadani E. 1982. The status of *Littorina aestuarii* Jeffreys. An approach using morphology and biochemical genetics. *J. Conchol.* 31:7-15
 156. Murphy PG. 1978. *Colisella austrodigitalis* sp. nov.: a sibling species of limpet (Acmaeidae) discovered by electrophoresis. *Biol. Bull.* 155:193-206
 157. Murray T. 1979. Evidence for an additional *Littorina* species and a summary of the reproductive biology of *Littorina* from California. *Veliger* 21: 469-74
 158. Nishida M, Lucas JS. 1988. Genetic differences between geographic populations of the Crown-of-thorns starfish throughout the Pacific region. *Mar. Biol.* 98:359-68
 159. Nizinski MS. 1989. Ecological distribution, demography and behavioral observations on *Periclimenes anthophilus*, an atypical symbiotic cleaner shrimp. *Bull. Mar. Sci.* 45:174-88
 160. Olsen JL, Stam WT, Bot PVM, van den Hoek C. 1987. scDNA-DNA hybridization studies in Pacific and Caribbean isolates of *Dictyosphaeria*

- cavernosa* (Chlorophyta) indicate a long divergence. *Helgol. Meeres.* 41:377–83
161. Palumbi SR. 1992. Marine speciation on a small planet. *TREE* 7:114–17
 162. Palumbi SR, Benzie J. 1991. Large mitochondrial DNA differences between morphologically similar penaeid shrimp. *Mol. Mar. Biol. Biotech.* 1:27–34
 163. Palumbi SR, Metz EC. 1991. Strong reproductive isolation between closely related tropical sea urchins (genus *Echinometra*). *Mol. Biol. Evol.* 8:227–39
 164. Palumbi SR, Wilson AC. 1990. Mitochondrial DNA diversity in the sea urchins *Strongylocentrotus purpuratus* and *S. droebachiensis*. *Evolution* 44: 403–15
 165. Parker ED Jr., Burbanck WD, Burbanck MP, Anderson WW. 1981. Genetic differentiation and speciation in the estuarine isopods *Cyathura polita* and *Cyathura burbancki*. *Estuaries* 4: 213–19
 166. Paxton H. 1979. Taxonomy and aspects of the life history of Australian beachworms (Polychaeta: Ronuphidae). *Aust. J. Mar. Freshw. Res.* 30:265–94
 167. Pfannenstiel H-D, Grünig C, Lucht J. 1987. Gametogenesis and reproduction in nereidid sibling species (*Platynereis dumerilii* and *P. massiliensis*). *Biol. Soc. Wash. Bull.* 7:272–79
 168. Raffaelli D. 1982. Recent ecological research on some European species of *Littorina*. *J. Mollusc. Stud.* 48:342–54
 169. Ramberg JP, Schram TA. 1982. A systematic review of the Oslofjord species of *Polydora* Bosc and *Pseudopolydora* Czerniavsky, with some new biological and ecological data (Polychaeta: Spionidae). *Sarsia* 68:233–47
 170. Reitner J, Keupp H, ed. 1991. *Fossil and Recent Sponges*. Berlin: Springer-Verlag
 171. Rice EL, Bird CJ. 1990. Relationships among geographically distant populations of *Gracilaria verrucosa* (Gracilariales, Rhodophyta) and related species. *Phycologia* 29:501–10
 172. Rice SA. 1991. Reproductive isolation in the *Polydora ligni* complex and the *Streblospio benedicti* complex (Polychaeta: Spionidae). *Bull. Mar. Sci.* 48: 432–47
 173. Rice SA, Simon JL. 1980. Intraspecific variations in the pollution indicator polychaete *Polydora ligni* (Spionidae). *Ophelia* 19:79–115
 174. Richmond RH. 1985. Variations in the population biology of *Pocillopora damicornis* across the Pacific. *Proc. 5th Int. Coral Reef Congr.* 6:101–6. Moorea, French Polynesia: Antenne Museum-EPHE
 175. Richmond RH. 1990. Relationships among reproductive mode, biogeographic distribution patterns and evolution in scleractinian corals. In *Advances in Invertebrate Reproduction*, ed. M Hoshi, O Yamashita, 5:317–22. Amsterdam: Elsevier
 176. Richmond RH, Jokiel PL. 1984. Lunar periodicity in larva release in the reef coral *Pocillopora damicornis* at Eniwetok and Hawaii. *Bull. Mar. Sci.* 34:280–87
 177. Robotti C. 1979. Electrophoresis of proteins in three populations of *Ophryotrocha labronica* La Greca e Bacci 1962 (Annelida Polychaeta). *Experientia* 35:596–97
 178. Rosenblatt RH, Waples RS. 1986. A genetic comparison of allopatric populations of shore fish species from the eastern and central Pacific Ocean: dispersal or vicariance. *Copeia* 1986:275–84
 179. Rowan R, Powers DA. 1991. A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbioses. *Science* 251: 1348–51
 180. Ryland JS, Tyler PA, ed. 1989. *Reproduction, Genetics and Distributions of Marine Organisms*. Fredensborg, Denmark: Olsen & Olsen
 181. Sarà M. 1990. Divergence between the sympatric species *Tethya aurantium* and *Tethya citrina* and speciation in sponges. In *New Perspectives in Sponge Biology*, ed. K Rützler, pp. 338–43. Washington, DC: Smithsonian Inst. Press
 182. Sarà M, Mensi P, Manconi R, Bavestrello G, Balletto E. 1989. Genetic variability in Mediterranean populations of *Tethya* (Porifera: Demospongiae). See Ref. 180, pp. 293–98
 183. Scheibling RE, Lawrence JM. 1982. Differences in reproductive strategies of morphs of the genus *Echinaster* (Echinodermata: Asteroidea) from the eastern Gulf of Mexico. *Mar. Biol.* 70:51–62
 184. Scheltema RS. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. Mar. Sci.* 39: 290–322
 185. Schopf TJM, Murphy LS. 1973. Protein polymorphism of the hybridizing seastars *Asterias forbesi* and *Asterias vulgaris* and implications for their evolution. *Biol. Bull.* 145:589–97

186. Schwenzer DE, Bulnheim H-P. 1991. Enzyme electrophoretic studies as a contribution to the systematics of the taxon *Tisbe* (Copepoda, Harpacticoida). *Z. Zool. Syst. Evolut.-Forsch.* 29:409-32
187. Seed R. 1992. Systematics evolution and distribution of mussels belonging to the genus *Mytilus*: an overview. *Am. Malac. Bull.* 9:123-37
188. Sévigny J-M, McLaren IA, Frost BW. 1989. Discrimination among and variation within species of *Pseudocalanus* based on the GPI locus. *Mar. Biol.* 102:321-27
189. Shaklee JB, Tamaru CS, Waples RS. 1982. Speciation and evolution of marine fishes studied by the electrophoretic analysis of proteins. *Pac. Sci.* 36:141-57
190. Shaw PW, Beardmore JA, Ryland JS. 1987. *Sagartia troglodytes* (Anthozoa: Actiniaria) consists of two species. *Mar. Ecol. Prog. Ser.* 41:21-28
191. Skadsheim A, Siegismund HR. 1986. Genetic relationships among north-western European Gammaridae (Amphipoda). *Crustaceana* 51:163-75
192. Smith PJ, Roberts PE, Hurst RJ. 1981. Evidence for two species of arrow squid in the New Zealand fishery. *NZ J. Mar. Freshw. Res.* 15:247-53
193. Smith PJ, Robertson DA. 1981. Genetic evidence for two species of sprat (*Sprattus*) in New Zealand waters. *Mar. Biol.* 62:227-33
194. Smith PJ, Wood BA, Benson PG. 1979. Electrophoretic and meristic separation of blue maomao and sweep. *NZ J. Mar. Freshw. Res.* 13:549-51
195. Smith RI. 1958. On reproductive pattern as a specific characteristic among nereid polychaetes. *Syst. Zool.* 7:60-73
196. Solé-Cava AM, Boury-Esnault N, Vacelet J, Thorpe JP. 1992. Biochemical genetic divergence and systematics in sponges of the genera *Corticium* and *Oscarella* (Demospongiae: Homoscleromorpha) in the Mediterranean Sea. *Mar. Biol.* 113:299-304
197. Solé-Cava AM, Klautau M, Boury-Esnault N, Borojevic R, Thorpe JP. 1991. Genetic evidence for cryptic speciation in allopatric populations of two cosmopolitan species of the calcareous sponge genus *Clathrina*. *Mar. Biol.* 111:381-86
198. Solé-Cava AM, Levy JA. 1987. Biochemical evidence for a third species of angel shark off the east coast of South America. *Biochem. Syst. Ecol.* 15:139-44
199. Solé-Cava AM, Thorpe JP. 1986. Genetic differentiation between morphotypes of the marine sponge *Suberites ficus* (Demospongiae: Hadromerida). *Mar. Biol.* 93:247-53
200. Solé-Cava AM, Thorpe JP. 1992. Genetic divergence between colour morphs in populations of the common intertidal sea anemones *Actinia equina* and *A. prasina* (Anthozoa: Actiniaria) in the Isle of Man. *Mar. Biol.* 112:243-52
201. Solé-Cava AM, Thorpe JP, Kaye JG. 1985. Reproductive isolation with little genetic divergence between *Urticina* (= *Tealia*) *felina* and *U. eques* (Anthozoa: Actiniaria). *Mar. Biol.* 85:279-84
202. Solé-Cava AM, Thorpe JP, Manconi R. 1991. A new Mediterranean species of *Axinella* detected by biochemical genetic methods. See Ref. 170, pp. 313-21
203. Solignac M. 1981. Isolating mechanisms and modalities of speciation in the *Jaera albifrons* species complex (Crustacea, Isopoda). *Syst. Zool.* 30:387-405
204. Southward AJ. 1976. On the taxonomic status and distribution of *Chthamalus stellatus* (Cirripedia) in the north-east Atlantic intertidal barnacles of Britain. *J. Mar. Biol. Assoc. UK* 56:1007-28
205. Stanhope MJ, Connelly MM, Hartwick B. 1992. Evolution of a crustacean chemical communication channel: behavioral and ecological genetic evidence for a habitat-modified, race-specific pheromone. *J. Chem. Ecol.* 18:1871-87
206. Stanhope MJ, Leighton BJ, Hartwick B. 1992. Polygenic control of habitat preference and its possible role in sympatric population subdivision in an estuarine crustacean. *Heredity* 69:279-88
207. Stoddart JA. 1984. Genetic differentiation amongst populations of the coral *Pocillopora damicornis* off southwestern Australia. *Coral Reefs* 3:149-56
208. Stoddart JA. 1986. Biochemical genetics of *Pocillopora damicornis* in Kaneohe Bay, Oahu, Hawaii. *Hawaii Inst. Mar. Biol. Tech. Rep.* 37:133-50
209. Strathmann RR. 1990. Why life histories evolve differently in the sea. *Am. Zool.* 30:197-207
210. Sullivan B, Miller K, Singleton K, Scheer AG, Williams AB. 1983. Electrophoretic analysis of hemocyanins from four species of mud crabs, genus *Panopeus*, with observations on the ecology of *P. obesus*. *Fish. Bull.* 81:883-85
211. Sundberg P. 1984. Multivariate analysis of polymorphism in the hoploneurtean

- Oerstedtia dorsalis* (Abildgaard, 1806). *J. Exp. Mar. Biol. Ecol.* 78:1–22
212. Sundberg P, Janson K. 1988. Polymorphism in *Oerstedtia dorsalis* (Abildgaard, 1806) revisited. Electrophoretic evidence for a species complex. *Hydrobiologia* 156:93–98
 213. Templeton AR. 1989. The meaning of species and speciation: a genetic perspective. In *Speciation and Its Consequences*, ed. D Otte, JA Endler, pp. 3–27. Sunderland, Mass: Sinauer
 214. Thorpe JP, Beardmore JA, Ryland JS. 1978. Genetic evidence for cryptic speciation in the marine bryozoan *Alcyonidium gelatinosum*. *Mar. Biol.* 49: 27–32
 215. Thorpe JP, Ryland JS. 1979. Cryptic speciation detected by biochemical genetics in three ecologically important intertidal bryozoans. *Estuar. Coast. Mar. Sci.* 8:395–98
 216. Thorpe JP, Ryland JS, Beardmore JA. 1978. Genetic variation and biochemical systematics in the marine bryozoan *Alcyonidium mytili*. *Mar. Biol.* 49:343–50
 217. Thorpe JP, Ryland JS, Cornelius PFS, Beardmore JA. 1992. Genetic divergence between branched and unbranched forms of the thecate hydroid *Aglaophenia pluma*. *J. Mar. Biol. Assoc. UK* 72:887–94
 218. Tsuchiya M, Nishihira M. 1984. Ecological distribution of two types of the sea-urchin, *Echinometra mathaei* (Blainville), on Okinawan reef flat. *Galaxea* 3:131–43
 219. Tsuchiya M, Nishihira M. 1985. Agonistic behavior and its effect on the dispersion pattern in two types of the sea urchin, *Echinometra mathaei* (Blainville). *Galaxea* 4:37–48
 220. Turner K, Lyster TA. 1980. Electrophoretic variation in sympatric mud crabs from North Inlet, South Carolina. *Biol. Bull.* 159:418–27
 221. Tuttle RD, Lindahl R. 1980. Genetic variability in 3 co-occurring forms of the starfish genus *Othilia* (= *Echinaster*). *Experientia* 36:923–25
 222. Uehara T, Shingaki M. 1985. Taxonomic studies in the four types of the sea urchin, *Echinometra mathaei*, from Okinawa Japan. *Zool. Sci.* 2:1009 (Abstr.)
 223. Väinölä R, Hvilson MM. 1991. Genetic divergence and a hybrid zone between Baltic and North Sea *Mytilus* populations (Mytilidae: Mollusca). *Biol. J. Linnean Soc.* 43:127–48
 224. Väinölä R, Varvio S-L. 1989. Biosystematics of *Macoma balthica* in northwestern Europe. See Ref. 180, pp. 309–16
 225. Valentine JW, Jablonski D. 1983. Speciation in the shallow sea: general patterns and biogeographic controls. In *Evolution, Time and Space: The Emergence of the Biosphere*, ed. RW Sims, JH Price, PES Whalley, pp. 201–26. London: Academic
 226. Van den Berghe W, Bergmans M. 1981. Differential food preferences in three co-occurring species of *Tisbe* (Copepoda, Harpacticoida). *Mar. Ecol. Prog. Ser.* 4:213–19
 227. Van den Hoek C. 1987. The possible significance of long-range dispersal for the biogeography of seaweeds. *Helgol. Meeres.* 41:261–72
 228. Van Moorsel GWNM. 1983. Reproductive strategies in two closely related stony corals (*Agaricia*, Scleractinia). *Mar. Ecol. Prog. Ser.* 13:273–83
 229. Van Oppen MJH, Olsen JL, Stam WT, van den Hoek C, Wiencke C. 1993. Arctic-Antarctic disjunctions in the benthic seaweeds *Acrosiphonia arcta* (Chlorophyta) and *Desmarestia viridis/willii* (Phaeophyta) are of recent origin. *Mar. Biol.* 115:381–86
 230. Van Veghel MLJ. 1992. Reproductive aspects of *Montastrea annularis* morphotypes. (Abstr.) 7th Int. Coral Reef Symp., Guam, p. 105
 231. Van Veghel MLJ, Bak RPM. 1993. Intraspecific variation of a dominant Caribbean reef building coral, *Montastrea annularis*: genetic, behavioral and morphometric aspects. *Mar. Ecol. Prog. Ser.* 92:255–65
 232. Vermeij GJ. 1991. Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology* 17:281–307
 233. Vermeij GJ. 1992. Trans-equatorial connections between biotas in the temperate eastern Atlantic. *Mar. Biol.* 112: 343–48
 234. Volkmann B, Battaglia B, Varotto V. 1978. A study of reproductive isolation within the super-species *Tisbe clodiensis* (Copepoda, Harpacticoida). In *Marine Organisms: Genetics, Ecology, and Evolution*, ed. B Battaglia, JA Beardmore, pp. 617–36. New York: Plenum
 235. Ward PD. 1987. *The Natural History of Nautilus*. Boston: Allen & Unwin
 236. Ward RD. 1990. Biochemical genetic variation in the genus *Littorina* (Prosobranchia: Mollusca). *Hydrobiologia* 193:53–69
 237. Ward RD, Janson K. 1985. A genetic analysis of sympatric subpopulations of the sibling species *Littorina saxatilis*

- (Olivi) and *Littorina arcana* Hannaford Ellis. *J. Mollusc. Stud.* 51:86-94
238. Warén A, Klitgaard A. 1991. *Hanleya nagelfar*, a sponge-feeding ecotype of *H. hanleyi* or a distinct species of chiton? *Ophelia* 34:51-70
- 238a. Warwick T, Knight AJ, Ward RJ. 1990. Hybridisation in the *Littorina saxatilis* species complex (Prosobranchia: Mollusca) *Hydrobiologia* 193:109-16
239. Weinberg JR, Starczak VR, Jörg D. 1992. Evidence for rapid speciation following a founder event in the laboratory. *Evolution* 46:1214-20
240. Weinberg JR, Starczak VR, Mueller C, Pesch GC, Lindsay SM. 1990. Divergence between populations of a monogamous polychaete with male parental care: premating isolation and chromosome variation. *Mar. Biol.* 107: 205-13
241. West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* 58:155-83
242. West-Eberhard MJ. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20:249-78
243. Westheide W, Rieger RM. 1987. Systematics of the amphiatlantic *Microphthalmus-listensis*-species-group (Polychaeta: Hesionidae): facts and concepts for reconstruction of phylogeny and speciation. *Z. Zool. Syst. Evolut.-Forsch.* 25:12-39
244. Williams AB. 1983. The mud crab, *Panopeus herbstii*, s.l. Partition into six species (Decapoda: Xanthidae). *Fish. Bull.* 81:863-82
245. Williams AB, Felder DL. 1986. Analysis of stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). *Proc. Biol. Soc. Wash.* 99:517-43
246. Williams KA, Skibinski DOF, Gibson R. 1983. Isoenzyme differences between three closely related species of *Lineus* (Heteronemertea). *J. Exp. Mar. Biol. Ecol.* 66:207-11
247. Willis BL. 1990. Species concepts in extant scleractinian corals: considerations based on reproductive biology and genotypic population structures. *Syst. Bot.* 15:136-49
248. Willis BL, Babcock RC, Harrison PL, Wallace CC. 1992. Experimental evidence of hybridization in reef corals involved in mass spawning events. (Abstr.) *7th Int. Coral Reef Symp., Guam*, p. 109
249. Wilson RR Jr, Waples RS. 1983. Distribution, morphology, and biochemical genetics of *Coryphaenoides armatus* and *C. yaquinae* (Pisces: Macrouridae) in the central and eastern north Pacific. *Deep Sea Res.* 30:1127-45
250. Wilson RR Jr., Waples RS. 1984. Electrophoretic and biometric variability in the abyssal grenadier *Coryphaenoides armatus* of the western North Atlantic, eastern South Pacific and eastern North Pacific oceans. *Mar. Biol.* 80:227-37
251. Wilson WH Jr. 1983. Life-history evidence for sibling species in *Axiiothella rubrocincta* (Polychaeta: Maldanidae). *Mar. Biol.* 76:297-300
252. Woodruff DS, Carpenter MP, Saunders WB, Ward PD. 1987. Genetic variation and phylogeny in *Nautilus*. In *Nautilus: The Biology and Paleobiology of a Living Fossil*, ed. WB Saunders, NH Landman, pp. 65-83. New York: Plenum