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Hybridization in the Sea

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1. INTRODUCTION

1.1. Background and Definitions

Hybridization and hybrid zones have long been of interest to evolutionary biologists because they offer excellent opportunities to study speciation and processes which contribute to reproductive isolation by either pre- or post-zygotic mechanisms. Such processes include assortative mating, hybrid unfitness and gamete incompatibility, all of which are believed to contribute to speciation.

Perhaps surprisingly, the term "hybrid zone" has proved difficult to define because definitions often include or imply an underlying mechanism concerning the origin or maintenance of the zone which might not be appropriate in all cases (for example, inferences about the width of the zone or the fitness of the individuals within the zone). The most workable definition is that proposed by Harrison (1990, p. 72): hybrid zones are "interactions between genetically distinct groups of individuals resulting in at least some offspring of mixed ancestry. Pure populations of the two genetically distinct groups are found outside the zone of interaction." This is the definition of a hybrid zone that is employed in this review. Similarly, isolated instances of hybridization may be defined as the production of one or more individuals resulting from the interbreeding of two genetically distinct parental individuals. As will be seen, the frequency of isolated cases of hybridization in the sea is considerably higher than that for the existence of hybrid zones or swarms (the latter may be defined as a collection of individuals of mixed ancestry resulting from high levels of interbreeding of genetically distinct parental types accompanied by introgression).

In the last decade, hybrid zones have received much attention (e.g. reviews by Endler, 1977; Moore, 1977; Barton and Hewitt, 1985, 1989; Harrison, 1990; Arnold, 1992; Arnold, 1993). The various types of hybrid zones (clines, tension zones, mosaics, reticulates, etc.) and the factors responsible for the establishment and maintenance of such zones have been well documented and the reader is referred to these excellent reviews. It is not the intention of this paper to re-examine these ideas and concepts, but to provide new information about natural hybridization in the sea, a subject which has received very little attention.

It is both interesting and surprising that in the above-cited reviews only one author mentions natural hybridization in the sea, where it is stated that very few well-documented cases exist (Harrison, 1993, p. 111). Whilst it is true that more is known about natural terrestrial hybridization, and that a greater number of better-documented examples exist from the terrestrial environment, it is also true that natural hybridization in the sea is not an uncommon phenomenon. Clearly, data from studies which have looked at hybridization in the sea, which has an estimated volume of $137 \times 10^6\,\mathrm{km}^3$ and is the largest ecosystem on earth (Gage and Tyler, 1991), which covers over 71% of the planet (Briggs, 1991), and which contributes many unique phyla (May, 1988; Winston, 1992), must aid substantially our understanding of natural hybridization, its causes and effects.

Hybridization is often viewed as one of the most important steps in speciation because if interbreeding taxa do not fuse then they are thought to evolve mechanisms such as differential mate choice and/or gamete incompatibility to prevent hybridization and thereby promote speciation (e.g. Mayr, 1942). In the context of the marine environment, relatively little is known about speciation (Knox, 1963; Palumbi, 1992, 1994). The marine environment is continuous (Battaglia, 1957; Sara, 1985) and less ephemeral than other environments (Hubbs and Kuronuma, 1941). Furthermore, the kinds of relatively pronounced ecotones found in terrestrial systems are much less frequent in the marine environment. In conjunction with the often widespread dispersal potential of many marine species, genetic differences between spatially segregated populations are often slight (e.g. Skibinski *et al.*, 1983). It has, however, been noted that ecological heterogeneity (e.g. the intertidal zone, or brackish water regions), combined with (micro)geographic isolation, should promote adaptive differentiation and ultimately evolutionary divergence in the marine environment (Battaglia, 1957). This in turn can promote hybridization because, according to Harrison's (1990) definition, genetic differentiation is a prerequisite for hybridization and the formation of hybrid zones.

Examination of the disparate and sometimes obscure data pertaining to natural hybridization in the sea indicates that many patterns exist which must be explained for a better understanding of the process of hybridization itself, as well as to provide greater insight into speciation in the sea. The major intentions of this review are: (1) to point out that hybridization in the sea is not as rare as previously thought; (2) to draw attention to hybridization bias amongst certain groups of marine organisms; (3) to illustrate biogeographic and environmental patterns in the location of hybridization; (4) to compare marine hybridization with hybridization in other environments; and (5) to discuss marine hybridization in the context of fisheries science and conservation.

1.2. Scope of the Review

A relatively broad approach is adopted in this review to permit inclusion of as many examples of marine hybridization as possible. Examples are drawn from environmental conditions ranging from fully marine to estuarine. The inclusion of hybridization in estuaries is justified on the grounds that: (1) estuaries are ecologically important to many truly marine species for moulting, reproduction, feeding, as larval nursery grounds, etc.; and (2) these areas play an important role in promoting marine speciation. Instances of hybridization involving both anadromous (e.g. salmonids) and catadromous (e.g. eels) species are excluded because such animals either breed in fresh water or spend most of their lives in fresh water, and are therefore not subject to the same evolutionary pressures as truly marine organisms. The scope of the review ranges from isolated examples of natural hybridization involving the production of a single (usually infertile) individual, through cases of marine hybrid swarms with associated high levels of introgression, to cases of speciation involving chromosome doubling. Although I have included as many examples as are known to me, this review is not exhaustive. Because of the subject matter (isolated instances of possible hybridization do not rank very highly on the scale of "publishability"), much of this information is obscure, and the reader may be familiar with examples which are not included here. My intention has been to draw from as many examples as possible to gain an overview of marine hybridization, its patterns, biases and effects.

In a limited number of instances it is difficult to determine if natural hybridization does indeed occur because of conflicting reports in the literature. For example, the cockles *Cerastoderma edule* and *C. glaucum* occur sympatrically in north-west Europe (Brock, 1979; Gosling, 1980), and it has been suggested that individuals which are morphologically intermediate between these two good species are natural hybrids (Kingston, 1973). Elsewhere, evidence suggests that hybridization is not the explanation for this morphological intermediacy (Brock, 1978; Gosling, 1980). In a case such as this, despite some evidence of hybridization, the example is not included in the review because the majority of evidence indicates that natural hybridization does not occur between these two species.

A more recent example of differences in opinion concerning the possible occurrence of hybridization involves the seerfishes *Scomberomorus commerson* and *S. guttatus*. According to Srinivasa Rao and Lakshmi (1993) these two species interbreed off the south-east coast of India to produce a hybrid which was previously recognized as *S. lineolatus*. Collette (1994) objects strongly to this interpretation, but because the data presented by both sides are osteological as opposed to biochemical (e.g. allozyme variation) or molecular (DNA sequence data) it is difficult to judge the validity of either argument. This example is included in the present review for the sake of completeness without lending weight to either opinion.

Finally, it is apparent that many of the records of marine hybridization involve isolated instances of hybridization without any evidence of the existence of a marine hybrid zone. These records are included in the review along with the better-documented cases of hybrid zones and hybrid swarms, because they provide a valuable supplement to these data.

2. RECOGNITION OF HYBRIDIZATION

2.1. Theoretical Considerations

Mayr (1979, p. 113) recognized five levels of hybridization (the first four of which grade into one another) regardless of the environment in which the hybridization occurs:

1. Infrequent interbreeding of sympatric species resulting in the production of hybrid offspring that are unable, for ecological or behavioural reasons, to backcross to one or both of the parental species.
2. Frequent or occasional interbreeding of sympatric species resulting in the production of at least partially fertile offspring, some of which backcross to one or both parental species.
3. Partial interbreeding between two formerly geographically isolated populations which failed to acquire complete reproductive isolation resulting in the formation of a secondary zone of contact.
4. Extensive interbreeding, resulting from the complete breakdown of reproductive isolation between sympatric species which produces a hybrid swarm in which the complete range of parental viabilities may be observed.
5. Interspecific hybridization in which a new species is produced as a result of chromosome doubling (allopolyploidy). This case is virtually restricted to plants (this might reflect a bias in our knowledge rather than a genuine phenomenon).

A review of the literature indicates that examples of all five of the cases proposed by Mayr (1979) have been reported from the marine environment. It is impossible, however, to estimate the frequency with which each category occurs because many reports of marine hybridization provide too few details for a judgement to be made. The important point here is that the full range of hybridization, from instances which result in the production of a single infertile offspring, to the production of new species, have been reported from the sea. A summary of cases detailing natural hybridization in the sea is provided in Table 1 (page 56) along with information concerning the geographic location and biogeographic region (according to Briggs, 1974) of the hybridization event, as well as details pertaining to the causes and outcomes (if any) of the event. These data are discussed in greater detail in subsequent sections.

2.2. Practical Considerations

Most studies of hybridization in the sea have looked at morphological variation: this is often the primary, and sometimes the only criterion used to identify hybrids (see Table 1). Due to the blending nature of hybridization, hybrids are usually morphologically intermediate between the two parental taxa in most characters examined (Mayr, 1979; Campton, 1987, 1990). This can be expressed in two ways: the hybrid can be morphologically intermediate between the parental types for each character (e.g. possesses 46 vertebrae when the parental types possess 48 and 44), or can possess one suite of characters which are typical of one parent and at the same time possess a suite of different characters which are typical of the other parent. Both types of intermediacy are reported in cases of marine hybridization.

Protein electrophoresis has proved to be a particularly valuable tool by which hybrids and individuals of mixed ancestry can be identified. This technique permits an objective evaluation of the hybrid status of individuals when the two hybridizing taxa are fixed for electrophoretic differences at one or more allozyme loci. However, it is sometimes the case that no fixed allelic differences exist between hybridizing taxa (all differences are a matter of allele frequency differences), which makes it that much harder to quantify the hybridization because all genotype combinations are theoretically possible within "pure" populations of the taxa. Arguably the best approach to this problem is to determine the conditional probability of any given genotype and then to determine whether or not this genotype occurs at the expected frequency (Campton and Utter, 1985; Gardner, 1996; Miller and Benzie, submitted).

Other techniques which have been utilized to identify natural hybrids or to investigate the dynamics of natural hybridization in the sea include investigation of haemoglobin patterns (Sick *et al.*, 1963), sperm agglutination tests (Vasseur, 1952), cytogenetics (Menzel and Menzel, 1965; Gray *et al.*, 1991 and references therein), mitochondrial DNA variation (Skibinski, 1985; Edwards and Skibinski, 1987; Gardner and Skibinski, 1991b), immunology (Owen *et al.*, 1971) and behavioural differences (Feddern, 1968; Dahlberg, 1970; Ayling, 1980).

Hybrid indices are often employed in the identification and characterization of hybridization (e.g. Gosline, 1948; Feddern, 1968). The benefit of such indices is that variation in a number of different traits (e.g. morphometric, behavioural, electrophoretic, coloration) can be summed to give an overall score for each individual, and thereby permit an evaluation of the total amount of variability between individuals. Individuals with the highest and lowest index scores are parental types (this is confirmed by the application of this technique to pure individuals of the taxa under investigation), and individuals with intermediate scores are hybrids.

The application of hybrid indices has been largely superseded by the application of multivariate statistical techniques such as principal components analysis and canonical discriminant analysis to the description of morphometric and genetic (electrophoretic) variation (e.g. Boitard *et al.*, 1980, 1982; Skibinski, 1983; McDonald *et al.*, 1991; McClure and McEachran, 1992; Srinivasa Rao and Lakshmi, 1993; Gardner, 1996). When the first two components of the analysis explain a large proportion of the variability in the data set, then plots of principal component 1 (PC1) versus PC2, or canonical variate 1 (CV1) versus CV2, can identify parental types as relatively discrete clusters of points, the distance between which is maximized by the analytical technique. Falling somewhere between these two extremes would be the hybrids and other individuals of mixed ancestry. Sometimes this results in a continuum from one parental type to another through many intermediate stages (e.g. hybrid *Mytilus edulis* and *M. galloprovincialis* mussel populations from south-west England (Gardner, 1996)) or can be represented by three relatively discrete clusters in which the two parental-type clusters overlap only slightly with the hybrid cluster (e.g. seerfish populations in the Bay of Bengal, India (Srinivasa Rao and Lakshmi, 1993; but see Collette, 1994)).

3. THE IMPORTANCE OF TAXONOMY

3.1. Systematics, Taxonomy and Hybridization

The systematic relationships (the study of the relatedness of organisms reflecting their respective evolutionary histories) and taxonomy (the names given to organisms reflecting their systematic relationships) of species are constantly being revised in light of new data. Clearly, taxonomy plays an important role in the defining of hybrid zones. This point was emphasized by Mayr (1979, p. 118) for hybrid swarms: "A thorough knowledge of the taxonomy of the respective groups is a prerequisite for a sound analysis of such situations. This is presumably the reason why so few such cases have so far been described . . .". The recent discovery of numerous marine sibling species has emphasized still further the importance of correct taxonomy based upon sound systematics. In their review of coral reef niche partitioning and the taxonomy of reef-dwelling organisms, Knowlton and Jackson (1994) point out that for many animal groups the number of sibling species is far higher than previously suspected. Despite only small-scale differences in behaviour, morphology, colour patterns and genetics, concordant patterns of variation from distinct geographic locations support the erection of specific status for many of these organisms. Similar findings are reported by Knowlton (1993) who extended the discussion of sibling species from the reef ecosystem to the entire marine environment. One of the main conclusions from these works is the necessity for the rigorous application of taxonomy to all marine systems. The study of marine hybrid zones is hindered by poor taxonomy: it is important that marine hybrid zones receive due attention because this will substantially improve our understanding of evolutionary processes and systematics in the marine environment.

Laboratory-based hybridization studies can provide a valuable means by which conspecifics can be recognized when it is considered that their present systematic status is incorrect. For example, Warwick *et al.* (1990) used laboratory interbreeding experiments to test the specific status of *Littorina rudis* and *L. saxatilis* (Prosobranchia: Mollusca) collected from Venice lagoon and south-west England. Because these two previously recognized species were able to produce viable offspring from reciprocal crosses between them, the authors concluded that *L. rudis* is a junior synonym of *L. saxatilis*.

In some instances, a previously recognized species has been identified as the product of natural hybridization. For example, off the Pacific coast of the USA and Canada, the flounder *Inopsetta ischyra* has been recognized as a hybrid between the starry flounder *Platichthys stellatus* and the English sole *Parophrys vetulus* (Schultz and Smith, 1936; Herald, 1941; Hart, 1973), and in the Bay of Bengal, India, the seerfish or Spanish mackerel *Scomberomorus lineolatus* has been identified as the product of the *S. commerson* × *S. guttatus* cross (Srinivasa Rao and Lakshmi, 1993; but see Collette, 1994). In these two cases it is probable that the recognition of both "species" as hybrids was only possible because of the large catch sizes of these commercially important species. An example of a non-commercial fish "species" now being recognized as a hybrid is provided by Randall (1956). The surgeon fish *Acanthurus rackliffei* from Hull Island, an atoll in the Phoenix Islands, Oceania, is now thought to be a hybrid between the closely related *Acanthurus achilles* and *A. glaucopareius*. In cases such as these, the recognition of interspecific hybrids which had been afforded specific status has assisted considerably in the understanding of evolutionary relationships which had been clouded by incorrect taxonomy between these closely related organisms.

3.2. Species Concepts and Hybridization

Harrison's (1990) definition of a hybrid zone, as provided earlier, makes no assumptions about the origin or structure of the hybrid zone. This definition also makes no assumptions about the specific status of the taxa involved in the interaction, other than to stipulate that some degree of genetic differentiation must exist between them. Certain species concepts are not so liberal, although many of the newer species concepts promote the idea that species are evolutionary dynamic entities and not static elements. In the following section, hybridization is assessed briefly in the light of different species concepts. This topic might be considered as worthy of review in its own right. Excellent treatments are available in Mayr (1970), Grant (1971), Carson (1975), Wiley (1981), Cracraft (1983, 1989), Templeton (1989), Avise and Ball (1990), Wallace and Willis (1994) and Mallet (1995), amongst others.

The Biological Species Concept (BSC), as championed by proponents such as Mayr (1970), is founded on the idea that taxa are reproductively isolated from each other, primarily by intrinsic (genetic) rather than extrinsic (geographical separation) factors. This is a relatively strict interpretation of the species since it views a species as a closed system. Based upon the BSC, no two interbreeding taxa which produce fertile offspring can be viewed as discrete species, because they are not, according to the definition, reproductively isolated (there are 32 examples of hybrid crosses which result in fertile offspring presented in Table 1). Yet the specific status of most of the taxa listed in Table 1 would be likely to satisfy the majority of biologists. Other major criticisms of the BSC are that: (1) it lacks a phylogenetic perspective sufficient to aid in the understanding of the origins and evolutionary histories of the species; (2) the concept does not apply well to plants; and (3) it is not heuristic (Sokal and Crovello, 1970; Grant, 1971; Price, 1996).

The Evolutionary Species Concept (ESC) views an evolutionary species as "a lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary and historical fate" (Wiley, 1981, p. 25). As far as the ESC is concerned, hybridization is unimportant: the important consideration is whether or not the two species "maintain their separate identities, tendencies and fates" (Wiley, 1981, p. 27). The ESC has been criticized on the grounds that the very traits which are important in defining species are themselves undefined (Templeton, 1989). This means that phenotypic variation within an organismal group can be interpreted in a variety of different ways, i.e. it is subjective. Gardner (1992) noted that where the blue mussels *M. galloprovincialis* and *M. edulis* hybridize extensively in western Europe, it is often impossible to distinguish between the two taxa because there is so much character overlap. The ESC thus fails to identify parental, hybrid and backcross mussels. The individual identities, tendencies and fates of these lineages is therefore called into question. However, this shortcoming is unlikely to apply in the majority of hybridization cases of Table 1.

The Phylogenetic Species Concept (PSC) defines a species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft, 1983, p. 170). Cracraft (1983, p. 172) notes that ". . . even if two sister-taxa hybridize, both can still be considered to be species if each is diagnosable as a discrete taxon . . . The critical point is that both species have had a distinct phylogenetic and biogeographic history prior to hybridization . . .". McKitrick and Zink (1988) suggest that hybridization between taxa simply indicates that reproductive isolation is not yet complete. The PSC places very little emphasis upon reproductive isolation but considerable emphasis on diagnostic characters. Avise and Ball (1990, p. 48) have criticized the PSC on the grounds that the number of species recognized depends on the resolving power of the tools available: "If each individual organism is genetically unique at a high level of resolution, then the grouping of individuals requires that we ignore distinctions that occur below some arbitrary threshold. The evolutionary significance of any such threshold must surely be questionable." With regard to hybridization, the PSC can only be judged to be useful in cases where truly diagnostic characters exist between species. This is not the case, for example, with smooth shelled blue mussels which exhibit frequency differences, but not absolute differences, for all traits so far investigated (Gardner, 1992, 1994).

The Recognition Species Concept (RSC) emphasizes mate-specific recognition systems of sexually biparental, eukaryotic reproduction. The species is defined as "that most inclusive population of individual biparental organisms which share a common fertilization system" (Paterson, 1985, p. 25). Thus, individuals of a species share common courtship behaviour, timing of reproduction, coloration, gamete compatibility, etc., in fact any and all components which contribute to reproductive success. The major limitations of the RSC are its sole application to bisexual eukaryotes but to no other biotic groups, and the poor fashion in which it deals with the syngameon, the most inclusive unit of interbreeding in a hybridizing species group (Templeton, 1989).

The Cohesion Species Concept (CSC) defines a species as "the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Templeton, 1989, p. 12). Cohesion mechanisms include processes such as gene flow, reproductive isolation, developmental constraints, and stabilizing selection. The CSC builds upon the foundation of other species concepts by emphasizing the mechanisms that produce and maintain species cohesion. The CSC is a wide-ranging species concept which is equally well applied to asexual species as it is to sexual species. Perhaps the greatest limitation with the CSC is that the cohesive mechanisms themselves are often poorly understood and require much more attention. Because the CSC ranges in its applicability from asexual taxa at one extreme to the syngameon at the other, hybridization can be easily handled by the concept.

The general historical trend in species concepts appears to have involved a move away from a rigid view of species as closed systems (for example, the BSC), towards a more flexible view of species as evolutionary dynamic entities (in particular, the CSC). With this change, though, has come increasing recognition that the concept of hybrids and hybrid zones is less clear-cut than had previously been thought. A universally applicable species concept must be able to include and explain hybridization, just as it must be able to cope with asexual reproduction. On this score, several of the species concepts fall down. Those that come closest appear to be the Evolutionary Species Concept and, in particular, the Cohesion Species Concept. This review of marine hybridization is not based solely on the species definition of one species concept, but does tend to favour the CSC definition.

4. FACTORS PREVENTING OR PROMOTING MARINE HYBRIDIZATION

4.1. Factors Preventing Hybridization

Harrison's (1990) definition of a hybrid zone states that some degree of genetic differentiation must exist between the two interbreeding taxa before hybridization can be considered to have taken place. Yet many marine populations are characterized by high levels of genetic similarity over very large distances. This genetic homogeneity is usually attributed to high levels of gene flow between populations which results from the considerable dispersal potential of the juvenile (pre-metamorphosis and/or pre-settlement) phase of the organisms concerned. Such high levels of gene flow, and the associated relative absence of genetic heterogeneity, will tend to reduce the frequency with which hybridization can occur. Furthermore, many marine populations are very large (millions of individuals), which will slow genetic divergence between these populations (Palumbi, 1994). These factors will tend to reduce the possibility of hybridization in the sea.

4.2. Factors Promoting Hybridization

Physical factors which promote hybridization in the sea usually involve environmental heterogeneity. Battaglia (1957) points out that ecological heterogeneity in the sea (preferably associated with isolation since habitat segregation is an effective reproductive isolating mechanism (Mayr, 1979)) is the most effective source of adaptive differentiation, and subsequent genetic divergence. Freshwater input, for example, interrupts the continuity of the sea and introduces isolating factors and selective forces which may be sufficiently intense to form locally adapted genetic variants (Battaglia, 1957). The extent of this genetic heterogeneity can range from local races, through sub- and semi-species, to full species, depending upon the strength of the effect of the freshwater input and the time-scale involved. Ultimately, differences in salinity between geographically neighbouring regions can be sufficient to promote reproductive isolation. For example, amphipod species of the genus *Gammarus* which occur on either side of the Baltic Sea and North Sea salinity discontinuity are now reproductively isolated, not because of the distance between them, but because of the salinity tolerance differences that exist between them (Kolding, 1985). Thus, genetic heterogeneity can result from environmental heterogeneity, which in turn can lead to hybridization at the boundaries of the environmental discontinuity before reproductive isolation is established (if it ever is established).

The intertidal zone is a region which is typified for its occupants by high levels of physiological stress associated with extremes of environmental variability, and as such is a region which can exert a severe selective pressure (Battaglia, 1957). In many places, the vertical distance between the top and the bottom of the intertidal region is no more than 2 m, but this short distance encompasses a wide range of habitat types. The very narrowness of the intertidal zone will tend to bring organisms into contact. For example, isopods of the genus *Jaera* are limited to the intertidal region where it is possible to find up to four species co-occurring, each separated from the others on a micro-geographic scale by ecological preferences (Solignac, 1976). However, because these species are mobile, encounters between them inevitably occur in such a small area, and such encounters can lead to hybridization, for example, in regions of north-west Europe (see Table 1, p. 70).

The majority of cases of hybridization of plants and invertebrates listed in Table 1 (p. 70) are reported from intertidal populations (very few fish species are strictly intertidal, and therefore examples of marine hybridization involving fishes are entirely restricted to regions other than the intertidal zone). Of the 57 non-vertebrate examples given, 31 occur in the intertidal zone and a further 17 occur in the shallow subtidal region (< 30 m below chart datum). To some extent these figures are a reflection of our familiarity with intertidal and shallow subtidal biota, but at the same time it is significant that the intertidal and shallow subtidal zones constitute only a minute percentage of the area of the marine ecosystem, and are therefore disproportionately highly represented. These data indicate a real propensity for hybridization amongst intertidal and shallow subtidal organisms, a phenomenon which is apparently related to the high degree of environmental variability of this region. Whether or not environmental heterogeneity has a similar effect upon fishes and other vertebrates is difficult to ascertain. Hybridization amongst both pelagic and benthic species is common, and since many fishes and marine mammals have wide ranges in their depth distributions it is difficult to draw any definitive conclusions concerning the influence of environmental heterogeneity upon the frequency of hybridization in these organisms.

Biological as well as physical factors will help to promote hybridization in the sea. A large number of sibling species (Knowlton, 1993) and species complexes are observed in the sea, with the result that individuals of these species have a high degree of genetic similarity to other such closely related species. This will help to promote hybridization (or at least will not assist the prevention of hybridization) because high levels of genetic similarity aid rather than prevent successful interbreeding.

In conclusion, the available data indicate that environmental heterogeneity plays an important role in promoting hybridization amongst plant and invertebrate species in the sea. Heterogeneous environments apparently promote and accelerate evolutionary processes which occur more slowly in other more uniform environments (Battaglia, 1957). No such conclusion can be reached for fish and mammalian species because too few data are currently available, and possibly because such a comparison cannot reasonably be made.

5. HOW FREQUENT IS HYBRIDIZATION IN THE SEA?

It is apparent that for two taxa to hybridize there must be, as a minimum, sufficient genetic compatibility between them to permit successful interbreeding, that is, to overcome the barriers of pre-zygotic reproductive isolation and post-zygotic genetic incompatibility.

High levels of genetic similarity characterize incipient species (which are undergoing speciation) and sibling species (which have recently diverged). Thus, regions with a high number of incipient or sibling species (such as coral reefs, represent "hot spots" for speciation, possibly resulting from increased niche partitioning amongst the coexisting species (Knowlton and Jackson, 1994)) would appear to be good potential locations in which to find marine hybrid zones. Knowlton (1993) has argued that sibling species are ubiquitous throughout the marine realm and, as a consequence, the possibility of observing natural hybridization in the sea should be good. However, it is often stated or indicated that natural hybridization in the sea is a rare phenomenon (Hubbs, 1955; Schwartz, 1972; Randall *et al.*, 1977; Mayr, 1979; Campton, 1987; Bert and Harrison, 1988). Campton (1990), in his review of the use of genetic markers in the analysis of hybridization in fisheries science, lists only two teleost and six invertebrate examples of marine hybridization, while Harrison (1990), in an excellent and extensive review of hybrid zones, mentions only one marine example.

One of the main reasons for considering hybridization in the sea to be such a relatively infrequent event probably stems from the fact that many examples involve one or only a few (< 10) hybrid individuals which have usually been determined by morphological intermediacy. Such descriptions often appear in the older literature or in non-mainstream publications, and for this reason can be easily overlooked. Despite the absence of data to confirm the genetic basis of the hybrid status of such individuals, it is clear that in most cases a long familiarity with a given species or group of organisms had been acquired by the authors before the hybrids were recognized (e.g. Owen *et al.*, 1971; Randall *et al.*, 1977).

Not surprisingly, many documented cases of natural marine hybridization involve commercially important species. Examples include hybrids between taxa of gadoids (Dymond, 1939), many flatfish (Norman, 1934 and references therein; Hubbs and Kurónuma, 1941; Fujio, 1977), clupeids (Dahlberg, 1969a and b, 1970; Turner, 1969), hard shell clams (Menzel, 1985; Hesselman *et al.*, 1988; Dillon, 1992; Bert *et al.*, 1993), blue mussels (Koehn *et al.*, 1984; Varvio *et al.*, 1988; Coustau *et al.*, 1991a; McDonald *et al.*, 1991; Freeman *et al.*, 1992; Sarver and Foltz, 1993), abalone (Owen *et al.*, 1971; Talmadge, 1977; Fujino *et al.*, 1980; Sasaki *et al.*, 1980; Brown, 1995), snow crabs (Karinen and Hoopes, 1971; Johnson, 1976; Grant *et al.*, 1977) and cetaceans (Cocks, 1887; Spilliaert *et al.*, 1991). Hybrids of lesser economic importance involve the capture and breeding of fishes for collectors, for example, the butterfly fishes (Randall *et al.*, 1977) and the angel-fishes (Pyle and Randall, 1994). It is more than likely that many of these examples of hybridization would not have been described if it was not for the fact that at least one of the taxa involved is commercially important. Consequently, very large sample sizes are available for examination, permitting the identification of hybrids which often occur naturally at very low frequencies.

The data presented in Table 1 (page 70) indicate that hybridization in the sea is not a rare event. There are 108 documented cases of hybridization listed, of which at least 34 involve hybrid zones or swarms, spanning the algae, higher plants, invertebrates and vertebrates. Thus, all major eukaryotic groups are represented (see later section for details). In their extensive review article, Barton and Hewitt (1989) examined over 170 non-marine hybrid zones, indicating that such hybrid zones outnumber marine hybrid zones by about 5 : 1. Approximately 1.4 million species have been identified from the earth, of which approximately 250 000 are marine (Winston, 1992 and references therein), giving a ratio of approximately 4.6 : 1 for non-marine to marine species. This is so close to the ratio of 5 : 1 quoted above, that it seems reasonable to conclude that hybridization (at least when measured in terms of the number of hybrid zones and hybrid swarms) in the sea occurs at the same frequency as hybridization in other environments. It must, however, be recognized that estimating the number of species in any environment is fraught with difficulty and unknown levels of inaccuracy derived from large-scale extrapolations of data collected from small-scale areas (for example see Briggs, 1991 and associated correspondence: Chaloner, 1992; Grassle, 1992; Briggs, 1992a and b).

In conclusion, whilst it is difficult to determine accurately the number of species in any given environment, the best data presently available indicate that rates of hybridization in the sea are surprisingly similar to those in, for example, the terrestrial environment. This fact has not been recognized previously, and it should not be overlooked when patterns and processes of hybridization are being investigated.

6. HYBRIDIZATION AND THE TIMING OF REPRODUCTION

Many authors have studied species-specific reproductive cycles to determine whether or not natural hybridization can possibly occur based upon overlap in the timing of reproductive activity. Such work usually involves an analysis of gonad index or histological examination of gonad maturity. This can be supplemented by plankton analysis which provides an indication of the similarity of spawning time of the two potentially hybridizing taxa based upon the co-occurrence of larval forms of the two taxa. This approach has been applied to populations of fucoid algae

(Burrows and Lodge, 1951), echinoderms (Chia, 1966; Hagström and Lonning, 1967; Schopf and Murphy, 1973; Strathmann, 1981), molluscs (Owen *et al.*, 1971; Seed, 1971; Dalton and Menzel, 1983; Dillon and Manzi, 1989; Gardner and Skibinski, 1990a), crustaceans (Jones and Naylor, 1971; Bert, 1985 cited in Bert and Harrison, 1988), corals (Miller and Babcock), flatfish (Hubbs and Kuronuma, 1941) and seerfish (Devaraj, 1986; Srinivasa Rao and Lakshmi 1993; but see Collette, 1994) to provide evidence supporting the occurrence of natural hybridization.

In other cases, investigation of natural reproductive cycles has indicated that there is in fact little or no overlap in the timing of reproductive activity, which would reduce substantially the opportunity for natural hybridization (e.g. Knight and Parke, 1950 for fucoid algae; Vasseur, 1952; Falk-Petersen and Lonning, 1983 for echinoderms; Dillon, 1992 for hard shell clams).

Clearly, the geographic locality and timing of sampling are of great importance. Periods of overlap in spawning activity between the sea urchins *Strongylocentrotus droebachiensis* and *S. pallidus* along the coast of Norway have been reported from some locations (Hagström and Lonning, 1967), but not at others (Falk-Petersen and Lonning, 1983), just as periods of reproductive overlap for the fucoid algae *Fucus vesiculosus* and *F. serratus* were recorded by Burrows and Lodge (1951) but not by Knight and Parke (1950) from different regions of the Irish Sea coast of England. Such reports reveal the importance of small-scale (in the order of kilometres) as well as larger-scale (hundredss of kilometres) spatial variability. Localized environmental conditions can dictate for two taxa the timing of reproductive activity which might be different at one location but overlap at a different location only a few kilometres away. Thus, hybridization is impossible at the first location but possible at the second location, at least within the time frame of the study (temporal variability in hybridization rates is discussed in a subsequent section). This sort of "mosaic" environmental effect upon reproductive cycles might be expected to have greatest effect in temperate regions where seasonality is most pronounced. In tropical regions, where environmental conditions are more stable, it might be expected that organisms are less likely to respond strongly to environmental cues for spawning activity. For example, Randall (1956) noted that the closely related surgeon fishes *Acanthurus achilles* and *A. glaucopareius* at Hull Island in Oceania do not exhibit definite spawning cycles so that specimens of both species collected at the same time have comparably developed gonads (Randall, 1956). Evidence from corals and other reef invertebrates, however, conflicts with this interpretation. Harrison *et al.* (1984) and Babcock *et al.* (1986, 1992) have shown that mass spawning events for these organisms in the Pacific and

Atlantic Oceans are highly predictable with respect to environmental cues. Whatever the situation, the absence of temporal reproductive isolation between closely related species will increase the chances of hybridization occurring.

Pronounced differences exist in the timing of reproductive activity of a species towards the limits of the distribution when compared with the timing of reproduction at the centre of distribution of that species. As a consequence, the amount of hybridization that occurs throughout the species range can be modified. For example, the amount of natural hybridization between the hard shell clams *Mercenaria mercenaria* and *M. campechiensis* in south-east USA is much less at Hamlin Creek, South Carolina, a site towards the northernmost limit of *M. campechiensis*, than it is further south at Indian River Lagoon, Florida, where the amount of spawning overlap is much greater (Dillon and Manzi, 1989; Dillon, 1992).

Finally, differences in size (and therefore also age) can determine the potential for hybridization between taxa, because individuals of a single species may reproduce at different times of the year as a result of size-dependent variation in the allocation of energy to somatic and gonadal growth. Gardner and Skibinski (1990a) have shown that amongst a hybrid population of the blue mussels *Mytilus edulis* and *M. galloprovincialis* in south-west England, different sized mussels of the same taxon spawn at different times. The greatest amount of overlap in the timing of spawning activity (and hence the greatest potential for hybridization) between the different size (= age) classes of the two taxa occurred between the largest *M. galloprovincialis*-like and the smallest *M. edulis*-like mussels. It was concluded that because these two mussel types exhibited greatest overlap in the number and timing of spawning events throughout the year that hybridization was a common occurrence. This finding is in agreement with an extensive allozyme data set which indicates the same (e.g. Seed, 1971; Skibinski, 1983; Gardner and Skibinski, 1988; Beaumont *et al.*, 1989).

7. EXPERIMENTAL HYBRIDIZATION

Laboratory hybridization experiments have been utilized extensively to confirm the probable hybrid nature of certain individuals by demonstrating that two taxa will interbreed when provided with the opportunity to do so, or that gametes from two taxa can be artificially cross-fertilized. Such information provides a valuable contribution to the study of natural marine hybridization. Many authors have demonstrated that hybridization in the laboratory can take place, thus providing evidence in support of the existence of natural hybrids. Such experiments have been carried out for marine algae (Burrows and Lodge, 1951; Bolwell *et al.*, 1977; Sanbonsuga and Neushul, 1978), molluscs (Loosanoff, 1954; Woodburn, 1961; Owen *et al.*, 1971; Leighton and Lewis, 1982; Dalton and Menzel, 1983; Beaumont *et al.*, 1993), echinoderms (Chia, 1966; Hagström and Lonning, 1961, 1967; Strathmann, 1981), crustacea (Solignac, 1976, 1978; Boitard *et al.*, 1980; Sekiguchi and Sugita, 1980) and corals (Willis *et al.*, 1992; Miller and Babcock, submitted).

Laboratory crosses have also demonstrated that there exists considerable potential for hybridization even among marine taxa which are no longer in geographic contact and therefore could not possibly hybridize in nature. Studies involving red algae from Scandinavia and the Gulf of Mexico (Rueness, 1973), kelp from the Canadian and European coasts of the North Atlantic (Luning *et al.*, 1978), from the west and south coasts of South Africa (Bolton and Anderson, 1987), from the North and South Atlantic Ocean (tom Dieck and de Oliveira, 1993), from the Atlantic and Pacific Oceans (tom Dieck, 1992), sea urchins from either side of the Isthmus of Panama (Lessios and Cunningham, 1990), wrasses from the North Atlantic and Mediterranean (Hagström and Wennerberg, 1964), gobies from either side of the Isthmus of Panama (Rubinoff, 1968) and North American and European lobsters (Mangum, 1993) have all demonstrated that despite geographic separation, hybridization is still possible, and in many cases easily attainable. These results demonstrate that relatively high levels of genetic similarity have been maintained and currently exist between these groups of geographically isolated species despite the long periods of time which have passed since the species were physically separated.

The closely related starfish species *Patiriella calcar*, *P. gunnii* and *P. exigua* occur sympatrically at numerous sites in New South Wales, Australia. Based upon the developmental outcome of laboratory hybridization crosses, Byrne and Anderson (1994) predict that viable natural hybrids between *P. calcar* and *P. gunnii* probably exist in wild populations along these coasts, but that interspecific hybrids involving *P. exigua* are unlikely to occur. Whilst there are no data to indicate the existence of such natural hybrids at present, the use of the laboratory hybridization technique can provide a powerful means by which the presence of natural hybrids may be predicted. This approach is most appropriate for cases in which the hybrid offspring are morphometrically very similar to one parental type, with the result that such hybrids are not easily recognizable and may therefore be overlooked.

8. TEMPORAL VARIABILITY AND STABILITY IN HYBRIDIZATION RATES

It is often assumed that hybrid zones are stable in time and space because theory indicates that this can be the case (Harrison, 1990). The number of studies which have looked at temporal variability in natural marine hybridization is small, but those that have can provide some valuable insights into this area.

Hybridization between the snow crabs *Chionecetes opilio* and *C. bairdi* varies both temporally and according to sex (Karinen and Hoopes, 1971). In 1969, hybrid males constituted 2.8% and hybrid females 1.6% of the populations in Bristol Bay in the south-east Bering Sea, but in 1970 these values had dropped to 1.0% and 0.4% decreases of 64% and 60%, respectively. Even larger changes in the percentage of hybrids have been reported for hybrids of the seerfishes *Scomberomorus commerson* and *S. guttatus* from the south-east coast of India (Devaraj, 1986; but see Collette, 1994). From Palk Bay and the Gulf of Mannar in 1967, hybrids represented 68% and 59% of the total populations, but in 1968 they represented zero and 5.6% of the catch (decreases of 100% and almost 91%, respectively). These two examples illustrate how much variability can exist in the dynamics of marine hybrid zones on short temporal scales. In neither case do the authors suggest why such pronounced temporal differences in the rate of hybridization might exist. It seems likely, however, that these differences reflect natural variation in ecological conditions resulting in, for example, variation in recruitment (especially since the seerfish hybrid zone is associated with up-welling which exhibits temporal variability in its onset), but may to some extent also reflect fishing pressure. They do, however, demonstrate the point that hybridization can be an ephemeral event when measured over short time-scales, for example, from one breeding season to the next.

Not all marine hybrid zones exhibit this degree of short-term temporal instability. Skibinski (1983) examined allozyme variation in two hybrid mussel populations (*Mytilus edulis* and *M. galloprovincialis*) from south-west England in 1980–1 and observed a pronounced length-dependent change in allele frequencies. In this case, alleles at highest frequency in allopatric *M. galloprovincialis* occurred at highest frequency amongst the largest mussels of the hybrid populations. When Gardner and Skibinski (1988) re-examined allozyme variation in these same two populations in 1986–7, they observed almost exactly the same pattern of variation as first described by Skibinski (1983). These findings were interpreted as evidence of short-term temporal stability because during this period six new generations had been added to each population. Maximum individual longevity was subsequently estimated to be about 12 years (Gardner *et al.*, 1993), but such longevity is achieved by very few mussels. In terms of mussel numbers, the turnover during this period would represent nearly all individuals (>99%). Thus, the populations examined by Skibinski (1983) had effectively been replaced by new mussels by the time they were examined by Gardner and Skibinski (1988).

Initial reports of natural hybridization between marine species in the early literature provide a means of estimating short-term periods over which hybridization is known to have occurred. In some cases it is possible to estimate the short-term (in)stability of hybridization events by comparing data between these various accounts. For example, Verrill (1909) reported that the starfish *Asterias epichlora* and *A. hexactis* (now *Leptasterias epichlora* and *L. hexactis*) hybridize freely in the vicinity of Puget Sound, on the Pacific coast of North America. Kwast *et al.* (1990) have shown that this is still the case. Hence, we can infer that this hybrid zone is relatively stable in the short term because, despite the addition of approximately 90 new generations, and the complete replacement of population numbers many times over during this period, the extent of hybridization between these two species is much as described at the start of this century.

Several reports exist of short-term hybridization amongst fishes, with hybrids being observed over periods of many decades, within the same geographical vicinity. Hubbs and Kuronuma (1941) reported collections of an intergeneric hybrid flatfish (*Platichthys stellatus* × *Kareius bicoloratus*) made in 1929 from Oshara on the east coast of Hokkaido, Japan. Fujio (1977) noted the presence of these same hybrids almost five decades later. The "hybrid flounder" *Inopsetta ischyra* (= *Parophyrs vetulus* × *Platichthys stellatus*) has been reported from several locations off the Pacific coast of the USA and Canada from 1880 onwards (Norman, 1934; Schultz and Smith, 1936; Herald, 1941; Hart, 1973 and references therein), and the hybrid seerfish *Scomberomorus lineolatus* (= *S. commerson* × *guttatus*) was first described in 1831 from the Bay of Bengal (Srinivasa Rao and Lakshmi, 1993). There is, however, some uncertainty as to the hybrid or specific status of this species (Collette, 1994).

The earliest confirmed report of marine hybridization that I am aware of involves the cetaceans *Balaenoptera musculus* (the blue whale) and *B. physalus* (the fin whale) off north Norway (Cocks, 1887). This report of 11 putative hybrids stems from the days of extensive whaling activity in the northern Atlantic. The application of modern molecular techniques has permitted the identification of a similar hybrid individual from waters off west Iceland (Spilliaert *et al.*, 1991) and suggests that hybridization between these two species might be wide-ranging in time and space.

It is extremely rare that we have a good idea of the time of the initial hybridization event between any two species. However, the example of hybridization between the sea grasses *Spartina maritima* and *S. alterniflora* provides a notable exception. The latter species was accidentally introduced into southern England sometime around 1830 and since about 1880 hybrids have been observed continually, indicating considerable stability in this hybrid zone over almost its entire duration (reviewed by Gray *et al.*, 1991).

The estimates of short-term temporal stability for hybridization gained by comparing reports from the literature encompass a wide variety of different organisms, including algae, invertebrates, fish and cetaceans, which suggests that short-term temporal stability of hybridization rates is the norm for most marine organisms.

Longer-term estimates of hybridization exist for two bivalve mollusc hybrid zones, one in western Europe, the other in North America. The first report of *M. galloprovincialis* in south-west England is by Donovan (1802): since *M. galloprovincialis* and *M. edulis* currently hybridize so readily in this region (reviewed by Gardner, 1994) one might assume that hybrids were likely to be present at the time of Donovan's report. Estimates of a time of genetic divergence between these two taxa are of the order of 1–1.5 million years as determined from biochemical variation (Skibinski *et al.*, 1980), suggesting that a long history of hybridization is likely. Probable hybridization between the hard shell clams *M. mercenaria* and *M. campechiensis* from south-east USA can be dated back even further. The fossil record indicates that both species were established in the Miocene, and have survived, apparently unchanged, for over 5 million years (Humphrey and Crenshaw, 1985; Dillon, 1992). Dillon (1992) suggested that these two clam species should be considered amongst the oldest of any extant species known to hybridize anywhere in the world. Harrison (1990), however, made the very telling point that simply because the environment in which present-day hybridization occurs has remained relatively stable for long periods of time does not necessarily mean that hybridization has been occurring for the same length of time. The stability of the environment does not tell us anything about the past distributions of the parental species, and whether or not they interbred. We must be cautious about inferring long-term stability for hybrid zones based only on information pertaining to environmental conditions. Unfortunately, this "paucity of real evidence will not be easy to remedy" (Harrison, 1990, p. 88). Given the caveat proposed by Harrison (1990) about inferring long-term stability of hybridization from environmental data alone, the examples outlined here provide the best evidence of long-term stability in marine hybrid zone location and composition. However, one method by which estimates of long-term hybridization rates may be obtained is by the application of multivariate statistical techniques to morphometric analysis of (sub)fossil specimens, where such a technique has been shown to be appropriate for living specimens. This would work well for both the *Mytilus* and the *Mercenaria* hybrid zones because the (sub)fossil records of these molluscs are relatively good. This approach would provide a meaningful way to address the question of long-term stability of hybridization, when this has proved to be so difficult to do for other species in other environments.

9. DISTURBANCE AND HYBRIDIZATION

9.1. Introduction

Disturbance, often as a man-made phenomenon, is recognized as an important factor contributing to hybridization (Stebbins, 1950; Mayr, 1979; Harrison, 1990). Of the 108 cases of marine hybridization recorded in Table 1 (page 70), 28 have reported the involvement of some form of disturbance (it is likely that more than this number involve disturbance, but reference to such an event is not made in every paper).

9.2. Human Disturbance

Deliberate or accidental introductions of taxa represent perhaps the ultimate example of human-mediated disturbance. Increasing awareness of the problems (both ecological and economic) associated with the introduction of "exotics" has opened the eyes of the scientific community to many of the risks that are now faced, particularly with the loss of genetic integrity of a native species resulting from hybridization and introgression with the exotic species.

One of the biggest threats to the integrity of native marine fauna and flora is the inadvertent transport of species over great distances, often in ballast water (Carlton and Geller, 1993). Laboratory experiments frequently demonstrate the potential for hybridization between species which are geographically isolated (and as a result could never hybridize in nature). It is likely that we will see rapid growth in the number of instances in which an accidental introduction results in hybridization between an exotic species and a native species.

A striking example of hybridization in the marine realm resulting from the accidental introduction of a species involves marsh grasses of the genus *Spartina* (reviewed by Gray *et al.*, 1991). *S. maritima* ($2n = 60$) is a common salt marsh plant in western Europe and elsewhere, and *S. alterniflora* ($2n = 62$) is a common marsh plant in North America. It is now thought that *S. alterniflora* was accidentally introduced into southern England from the USA sometime around 1830. Hybridization between the two species gave rise to *S. x. townsendii* ($2n$ with a mode of 62) which is a sterile hybrid. At an unknown date this event was followed by a chromosome doubling to produce a fertile amphidiploid form known as *S. anglica* ($2n$ ranges from 120 to 127, but is usually 120, 122 or 124). These grasses play an important role in stabilizing marsh and estuary sediments. As a result, they have been introduced from southern England to many different localities including France, Spain, China, Germany, Denmark, Australia and New Zealand. Because of the nature of the extensive coexistence of the various *Spartina* species within the salt marsh grass beds of southern England, it is quite possible that most, if not all, forms of these grasses have been transplanted to these other countries. Unfortunately, no information is available concerning the occurrence, structure and dynamics of introduced *Spartina* hybrid zones from any of these locations. This is an area for research which could prove particularly rewarding if pursued.

The opening up of new shipping ways such as the Suez Canal provides for considerable movement of organisms between previously isolated regions. Although in the Suez Canal significant salinity changes provide barriers to dispersal, movements of fauna through the canal are well documented. There has been extensive migration from the Red Sea to the Mediterranean Sea (the Lessepsian migration), but much less movement of organisms in the opposite direction (Briggs, 1974). At the moment no record of hybridization resulting specifically from migration via the Suez Canal or the Panama Canal has been reported, but such a phenomenon is a very real possibility. Hybridization has, however, been recorded in association with the Kiel Canal, or Nordostseekanal, which links the River Elbe in Germany to the Baltic Sea. Solignac (1976) has reported the presence of a hybrid swarm of *Jaera praehirsuta* × *ischiosetosa* (Crustacea: Isopoda) in the canal. It seems likely that the establishment of the canal has resulted in the hybridization of these two isopod species, but pre-existing natural hybridization is difficult to rule out because several other hybrid zones exist in this same geographical location.

Perhaps the most striking example of hybridization having deleterious effects upon species integrity resulting from the deliberate introduction of one or more species, involves the introduction of two Japanese oysters (*Crassostrea sikamea* and *C. gigas*) into California, USA (Hedgecock *et al.*, 1993). This example is dealt with in more detail in Section 19.

9.3. Natural Disturbance

Natural disturbance is recognized as an important factor contributing to hybridization (Hubbs, 1955). Two relatively common themes linking examples of marine hybridization involving natural disturbance are the influences of freshwater input (this can be in a fully saline context with occasional freshwater run-off, can take place in a permanent estuarine setting, or can be associated with the removal of a freshwater barrier) and up-welling.

Examples of marine hybridization which are known to be associated with freshwater disturbance include flatfish (Hubbs and Kuronuma, 1941), and isopods (Jones and Naylor, 1971; Solignac, 1976). Members of the isopod *Jaera albifrons* species complex in western Europe are known to hybridize infrequently at several sites, and frequently at only a small number of sites. It is possible to find up to four species at the same location, each separated from the others by ecological preferences, usually according to tidal height (Solignac, 1976). Jones and Naylor (1971) reported finding a single hybrid individual (*J. albifrons* × *ischiosetosa*) at Milford Haven, South Wales, in the bed of a dried stream leading to the intertidal zone. The temporary natural disturbance caused by the drying of the stream is thought to have permitted the migration of *J. ischiosetosa* into the microhabitat occupied by *J. albifrons*, and resulted in limited hybridization (the single hybrid represented 0.085% of the 1179 *albifrons* and *ischiosetosa* collected). Many other examples of hybridization are associated in some way with the effect of fresh water, often because one of the hybridizing taxa has an ecological preference for lower salinity than the other species involved (refer to Table 1, page 70). This can be viewed as a form of natural disturbance involving freshwater influence because the effect is often highly variable in time and space.

It is interesting to note that many cases of natural hybridization are reported from the Pacific coast of North America (especially southern California and Puget Sound) which is an area of permanent and extensive up-welling. Examples include kelp (Coyer and Zaugg-Haglund, 1982; Coyer *et al.*, 1992), echinoderms (Verrill, 1909; Swan, 1953; Chia, 1966; Strathmann, 1981; Kwast *et al.*, 1990), and molluscs (Owen *et al.*, 1971; McDonald *et al.*, 1991; Sarver and Foltz, 1993). It should be noted, however, that it is difficult to disentangle the effects of up-welling from other effects which might cause hybridization. Srinivasa Rao and Lakshmi (1993) have suggested that hybridization between the seerfish *Scomberomorus commerson* and *S. guttatus* in the Bay of Bengal, is coincident with the timing of the local up-welling event from February to April, which results in intermediate salinity between the low of December and the high of May. It is noted that the environmentally "intermediate conditions obtaining in January/February induce the ready-to-spawn adults of both putative parents, which may not normally hybridize, to breed irrespective of availability of proper mates, resulting in hybridization between the two species" (Srinivasa Rao and Lakshmi, 1993, p. 487; but see Collette, 1994). It is presently impossible to differentiate between two possibilities which might be responsible for the high level of hybridization observed in such regions, namely that the disturbance effect of the up-welling event itself, or that the increased primary productivity, which is thought to permit greater niche partitioning (and therefore ultimately speciation), is the causative factor.

Burrows and Lodge (1951) suggested that the removal of pure adult fucoid algae following the artificial clearance of intertidal regions at Port St Mary, Isle of Man, permited the establishment of competitively inferior hybrid sporelings which could not establish in the presence of the parental species. This hypothesis received support when a natural hybrid swarm of *Fucus spiralis* × *F. vesiculosus* from the River Mersey, north-west England, was recognized. This hybrid swarm exists on very soft sandstone which constantly and naturally erodes away once the weight of the established fucoids is too great to be maintained by the soft rock. This results in continual recolonization of the substratum with an associated short-term decrease in intraspecific competition from pure parental types which permits the establishment of the hybrid plants. Without this natural erosion it is unlikely that the hybrid individuals could become established.

Natural disturbance plays an important role in promoting hybridization of abalone species along the coast of California (Owen *et al.*, 1971). The authors note that "areas where an excessive number of hybrids were found had one thing in common, the presence of large populations of the sea urchin *Strongylocentrotus franciscanus* and a resulting destruction of nearly all algal cover, including the giant kelp, *Macrocyctis pyrifera*" (Owen *et al.*, 1971, p. 32). Over a 4 year period at a site south-west of Point Conception, California, sea urchin grazing completely destroyed a substantial area of kelp forest (kelp fragments provide an important food source, and the kelp forest habitat acts as a refuge and breeding ground for some abalone species). During this 4 year period the number of abalones decreased tenfold whilst the number of hybrids remained the same. The authors concluded that hybridization was most prevalent in areas subjected to habitat disturbances, probably because different species which are not normally in close contact could intermingle and interbreed.

The single phenomenon bring about the greatest incidence of hybridization in the sea is likely to be natural disturbance involving geological upheaval; for example, events such as the formation of the Florida peninsula or Pleistocene cooling associated with the last Ice Age. Such events tend to break up continuous biotic distributions into two or often many more fully or partially isolated subpopulations. Over time, these newly established allopatric populations accumulate genetic differences resulting from stochastic processes (genetic drift) and/or adaptation to the new localized environment (natural selection). When the barrier between the populations is removed and secondary contact is established the newly evolved races, subspecies, semi-species or full species are occasionally able to interbreed. This scenario for the formation of many hybrid zones (especially in temperate and terrestrial regions) has been invoked extensively and much evidence supports it (Harrison, 1990). Inspection of the data of Table 1 (page 70) indicates that such events do indeed have a profound effect upon the establishment of not just isolated hybridization events, but also upon hybrid zones and hybrid swarms. For example, many of the best-known marine hybridization events occur along the coasts of Florida, in north-west Europe and at the boundary between the North and Baltic Seas, areas which are known to have been substantially disturbed by geological upheaval, sea level regressions associated with Ice Age cooling, and salinity changes resulting from the formation of the new environment.

One of the greatest collections of marine hybrid zones is found along the coasts of the Florida peninsula and into the Gulf of Mexico. This region is known to represent a major discontinuity in the genetic composition of many species, some of which show continuous distributions around the peninsula (Reeb and Avise, 1990). The geological formation of the peninsula has been extensively documented (Walters and Robins, 1961; Avise, 1992) and the consequent effects upon biotic distributions have been profound. Clearly, the geological disturbance associated with the formation of the peninsula has been particularly important in the establishment of many marine hybrid zones.

In north-west Europe, the Pleistocene epoch is thought to have had a profound effect upon biotic distributions and the presence of many hybrid zones, both terrestrial and marine. Marine hybrid zones involving *Jaera* (Isopoda, Crustacea) (Jones and Naylor, 1971; Solignac, 1976, 1981), *Xantho* (Decapoda, Crustacea) (Almaça, 1972) and *Mytilus* (*M. edulis* × *galloprovincialis*) (Bivalvia, Mollusca) (Seed, 1971; Skibinski, 1983; Gardner and Skibinski, 1988; Gardner, 1994) are all likely to have originated as a result of secondary contact following the ice sheet regression. Other hybrid zones listed in Table 1 probably arose in this way, too.

Several hybrid zones and abrupt discontinuities in biotic distributions have been recorded from the region between the low-salinity Baltic Sea and the more fully saline North Sea. The present-day Baltic Sea is thought to have been established approximately 6000 years ago (Briggs, 1974) and consequently any unusual biotic effects have arisen since that time. Associated with the Belt and Baltic Seas are hybrid zones involving *Jaera* (Isopoda, Crustacea) (Solignac, 1976, 1981), *Macoma* and *Mytilus* (Bivalvia, Mollusca) (Varvio *et al.*, 1988; Väinölä and Varvio, 1989; McDonald *et al.*, 1991; Väinölä and Hvilsom, 1991) and *Platyichthys* × *Pleuronectes*, *Pleuronectes* × *Glyptocephalus* and *Scophthalmus* (Pleuronectidae, Pisces) (Norman, 1934).

Hewitt (1988) suggests that most hybrid zones are likely to have originated as a result of secondary contact. This is clearly an important mechanism by which hybrid zones in any environment, including the sea, can be generated. Many of the examples of marine hybrid zones given in Table 1 are likely to have arisen in this fashion, but may now be maintained by factors such as ecological differences between the taxa involved.

10. RELATIVE PARENTAL ABUNDANCE AND HYBRIDIZATION

It is often the case that hybridization is reported from areas where one parental type occurs at very low density. This situation would at first sight appear to mitigate against hybridization, but under certain circumstances it can in fact promote it. Individuals which occur at very low density, often beyond the usual distributional range of their species, will have difficulty in finding a conspecific mate. In such cases, Mayr (1979, p. 127) noted that in "the absence of adequate stimuli, that is, stimuli from conspecific individuals, they [lone individuals] are apt to respond to inadequate stimuli, that is to individuals belonging to a different species. Many of the known hybrids of animal species are found at the margin of the normal geographic range of one of the two parental species or even beyond it." This scenario applies equally to species with highly developed mate recognition systems as well as to species which are free-spawning and employ gamete recognition systems (or similar) as part of their reproductive biology.

Owen *et al.* (1971) have reported 12 of the 15 possible hybrid crosses between six abalone species from California. In several of these crosses, one parental type occurs at very low frequency at the limit of the species distribution. Amongst hybridizing stone crabs (*Menippe mercenaria* × *M. adina* from Florida, Bert and Harrison (1988) suggested that a large inequality in the numbers of the parental forms may have resulted in unusual patterns of carapace coloration and allozyme allele frequencies. Dillon (1992) reported hybrids at Hamlin Creek, South Carolina, between the southern hard shell clam *M. campechiensis* which is rare at this site and the northern clam *M. mercenaria* which is abundant. From approximately 10 000 *M. mercenaria* he identified 27 pure *M. campechiensis* and six hybrids and individuals of mixed ancestry, based upon electrophoretic criteria.

Randall *et al.* (1977) observed that the large majority of chaetodontid fishes involved in hybridization can be classified according to their behaviour as either solitary or occurring in pairs. Very little evidence was found of hybridization involving gregarious species which form spawning masses. These authors pointed out that at any given location it is expected that if a conspecific mate is unavailable then a solitary fish will seek to mate with an individual of a closely related species, rather than not reproducing at all: this is exactly what is observed. In this context, then, the occurrence of a single individual or small number of individuals outside the normal range of that species increases the probability of hybridization, provided that isolating barriers are not so well developed as to completely prevent interbreeding.

The social structure of the species in question may also be of importance in determining why individuals of one species interbreed with another species. For example, female angel-fishes of the genus *Centropyge* form harems and, within each harem, females are ranked according to their dominance. The most dominant females monopolize the male during optimal spawning times, often forcing subordinate females to spawn at suboptimal times (Pyle and Randall, 1994). It has been suggested (Pyle and Randall, 1994) that this might make a subordinate female choose to spawn with a heterospecific male at the optimal spawning time, rather than with a conspecific male at a suboptimal time. This does not explain why the male would want to mate with a subordinate (and therefore less fit) heterospecific female, but it does illustrate that under certain conditions, interspecific hybridization might be promoted by the breeding behaviour of at least one of the species involved.

11. THE FITNESS OF HYBRID INDIVIDUALS

There is a large body of evidence from detailed examinations of natural hybrid zones and from laboratory experiments indicating that hybridization often, if not usually, results in the production of infertile offspring, or individuals which possess a greatly reduced reproductive potential compared to the parental types. This can occur for a variety of reasons, but many of the best-documented examples involve hybrid dysgenesis, a phenomenon in which the hybrid individual is, amongst other things, unable to develop fully functional gonads (Kidwell, 1982; Lozovskya *et al.*, 1990; Heath and Simmons, 1991; Khadem and Krimbas, 1993). It is, however, possible that hybrid offspring are produced which are fertile but possess a much reduced reproductive potential compared to both parental types. This can result from the inability of the hybrid to attract a mate of either parental species if pre-mating behaviour is involved, because the hybrid individual produces a much reduced number of gametes, or because the gametes which are produced are not fully functional.

In the strictest sense, individual fitness means reproductive success only, but since many parameters influence reproductive success, fitness can also be used in a wider sense to mean any aspect of the biology of the individual concerned which affects reproduction. Examples of hybrid unfitness are plentiful in the marine biology literature and include slower rates of development (in echinoderms: Hagström and Lonning, 1961, 1967; in molluscs: Fujino *et al.*, 1980), decreased fertilization success (in echinoderms: Hagström and Lonning, 1961; Strathmann, 1981; in crustaceans: Solignac, 1976), lower individual fecundity or complete sterility (in marsh grass: Gray *et al.*, 1991; in crustaceans: Karinen and Hoopes, 1971; Johnson, 1976; in echinoderms: Swan, 1953; in flatfish: Holt, 1893; Norman, 1934), increased mortality rates (in algae: Coyer and Zaugg-Haglund, 1982; in echinoderms: Hagström and Lonning, 1961; in molluscs: Owen *et al.*, 1971), increased susceptibility to gonadal neoplasia (in molluscs: Hesselman *et al.*, 1988; Bert *et al.*, 1993), decreased competitive ability (in algae: Burrows and Lodge, 1951), increased morphological variability (in echinoderms: Kwast *et al.*, 1990), the absence of hybrid genotypes predicted from the presence of parental genotypes (in crustacea: Bert and Harrison, 1988), lower body size or weight (in echinoderms: Kwast *et al.*, 1990), highly skewed sex ratios (in fish: Turner, 1969; Dahlberg, 1970), and higher rates of parasitism (in fish: Turner, 1969).

Given that many hybrids are morphologically intermediate in one form or another, it is not surprising that hybrid fitness is also frequently reported as being intermediate between those of the parental types, or that the fitness parameter under investigation is no different from one or both of the parental types. Examples from the marine realm include developmental stability and developmental rate (in echinoderms: Chia, 1966; Strathmann, 1981; in molluscs: Gardner 1995), growth rate (in molluscs: Gardner *et al.*, 1993), body size (in echinoderms: Kwast *et al.*, 1990; in cetaceans (Cocks, 1887), fertility and fecundity (in marsh grass: Gray *et al.*, 1991; in crustaceans: Solignac, 1976, 1981; in echinoderms: Schopf and Murphy, 1973; in molluscs: Gardner and Skibinski, 1990a), viability (in crustaceans: Solignac, 1976; in molluscs: Menzel, 1985; Gardner and Skibinski, 1991a; Gardner *et al.*, 1993; Willis and Skibinski, 1992), chromosomal structure (in molluscs: Menzel and Menzel, 1965), allozyme thermostability (in molluscs: Gardner and Skibinski, 1990b) and resistance to parasites (in molluscs: Coustau *et al.*, 1991b).

In a smaller number of cases it has been reported that hybrids have a fitness advantage compared with both parental types; this can be viewed