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CHAPTER 19

Reproduction

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Introduction

An overview of fundamental natural and life histories must first set the stage for any comprehensive review of reproductive ecology. An expanded construct of more quantitative, behavioral and other, higher-order ecological information can then be built atop this base. We have therefore organized the present chapter into four major parts. We begin with a section on reproductive natural history providing summary data on reproductive modes and spawning types, courtship, and a taxonomic survey of their distributions. This brief review of key life history topics such as body size-related reproductive effort and tradeoffs between the number and size of offspring produced next leads to an in-depth section on the behavioral and evolutionary aspects of reproductive ecology focused on mating systems and gender allocation, sexual selection, and parental care. We follow this with a section that reviews the poorly recognized occurrence of secondary gonochorism in warm temperate representatives of several tropical fish lineages, and discuss the unusual Californian/eastern North Pacific preponderance of species with extensive investment in individual offspring (via viviparity and post-zygotic parental care in oviparous species). Both of these phenomena are interpreted in terms of differences between temperate and tropical reefs in benthic habitat persistence and on- versus off-reef predation risk to propagules and in environmental potentials for mate monopolization and related development of polygamous mating systems. Also considered is the possible influence of the temporally and spatially unpredictable upwelling regime of the eastern North Pacific. A concluding summary section identifies data deficiencies and suggests promising topics for future research, with special emphasis on the patterns of extensive and diverse maternal investment and parental care for which California marine fishes provide ideal subjects for comparative study.

The scope of this review is consistent with other chapters of this book: the primary geographic focus is on the fishes of California and the Pacific coast of Baja California. Habitat considerations within the marine realm span the intertidal to the abyssal, from the pelagic to the benthic; partly marine (estuarine and anadromous/catadromous species) as well as fully marine fishes are considered. The taxonomic scope includes all of the native California marine species of elasmobranchs and teleosts listed in Fitch and Lavenberg (1968), Miller and Lea (1972), and De la Cruz Aguero et al. (1997), with more recent species nomenclature following Eschmeyer (1998). Select exotics (including species purposely and accidentally introduced to the Californias) are used to further illustrate patterns. Species occurring in California are used as primary examples of patterns recognized from studies of fishes in other habitats and geographic regions of the world. Taxonomic relationships higher than the generic level follow Nelson (1994).

Reproductive Natural History

Taxonomic Survey of Reproductive Modes and Spawning Types

The fishes of the Californias and elsewhere represent two major modes of offspring production: 1) the direct production of juveniles that are miniature adults and 2) the indirect production of pre-juvenile stages (eggs, larvae). These two modes are really extremes on a continuum of parental investment in individual offspring. At one extreme, reproduction is oviparous, maternal provisioning is lecithotrophic (limited to the yolking of ovarian oocytes prior to fertilization), and zygotes develop outside of the maternal environment and independent of further energetic investment by either parent. The ova of egg layers are usually fertilized externally, but notable exceptions include the oviparous sharks (e.g., heterodontids and scyliorhinids) and skates (Rajidae), which lay horny egg cases after copulation and internal fertilization, and the scorpaeniform family Cottidae. At the other extreme, there is matrotrophic viviparity (live-bearing of young provisioned extensively beyond the nutrition provided by ovum yolk). This contemporary view of oviparity and viviparity as degrees of maternal investment distinguishable by birth mode alone removes the need for the outdated concept of ovoviviparity, once considered to be a discrete intermediate between the two extremes (Wourms et al., 1988). In strict ovoviviparity, embryos are provisioned entirely pre-fertilization even though some embryogenesis occurs internally. Recent

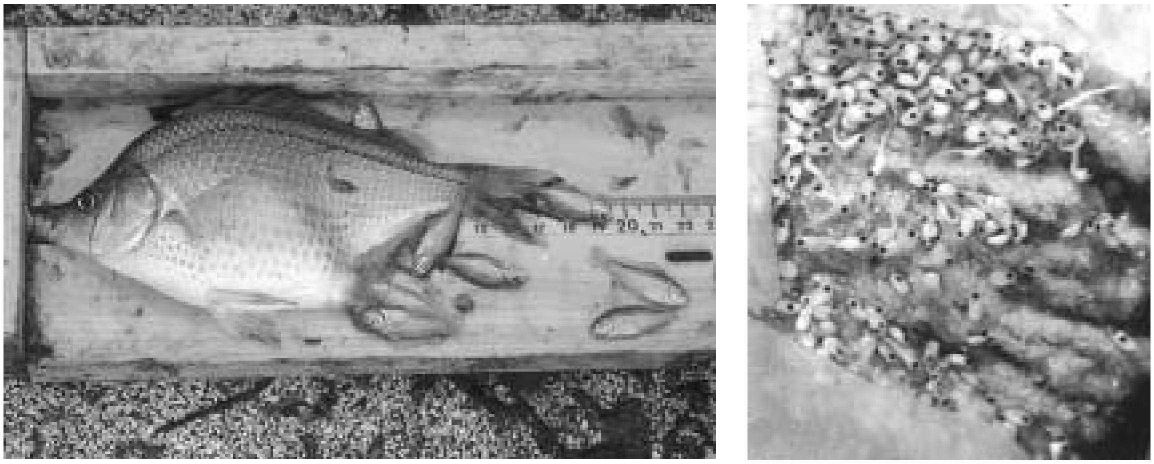

FIGURE 19-1 (A) Near-term female of the embiotocid *Hysterocarpus traski* aborting embryos upon capture; the length-specific fecundity of this freshwater species is the highest among embiotocids, followed by the marine species *Brachyistius frenatus* (Baltz, 1984). Photo by D. Baltz. (B) Pregnant female of the sebastine scorpaenid *Sebastes paucispinis* with ovarian embryos exposed by dissection (from Moser, 1967, with permission from Allen Press).

research has shown that ovoviviparity is not a discrete intermediate, but rather encompasses a broad range of provisioning post-fertilization (Wourms et al., 1988). Thus, we consider ovoviviparity as a less extreme type of viviparity, while acknowledging the existence of a range of intermediates along a continuum approaching matrotrophy.

Reproductive specialization has evolved from oviparity to viviparity independently within diverse lineages of elasmobranchs (sharks and rays) and teleosts (bony fishes) in California, as elsewhere (Wourms et al., 1988; Wourms and Lombardi, 1992). Viviparity ranges from the strictly lecithotrophic (live-bearing of young provisioned entirely by ovum yolk) to matrotrophic viviparity. The latter is an extreme type of parental care in which the developing young receive total protection within, as well as energy provisioning by, the mother. Examples of lecithotrophic viviparity include some sharks such as the spiny dogfish (*Squalus acanthias*) and perhaps some scorpaenids of the genus *Sebastes*. Extensive matrotrophic nourishment by yolk sac placentae occurs in certain viviparous sharks (some triakids and most carcharhinids including sphyrnines) and (via several types of placentae and placenta-like structures) in the viviparous brotulas (Bythitidae) and surfperches (Embiotocidae).

Of the four genera of bythitids known from California waters (*Ogilbia*, *Cataetyx*, *Grammonus* and *Brosmophycis*), viviparity has been documented for only one species, *B. marginatus* (Hart, 1973) but information on bythitids elsewhere indicates extensive matrotrophy in all genera (Wourms et al., 1988). In between the strict lecithotrophs and extreme matrotrophs occurs a continuum of provisioning, with the relative degree of embryo nourishment by ovum yolk and maternal-embryo nutrient exchange varying among families and species in both elasmobranchs and teleosts. Included are aplacental viviparity supplemented by production of nurse eggs for consumption by embryos (oophagy) in alopiid (thresher) and cetorhinid (basking) sharks and intrauterine cannibalism of sibling embryos (adelphophagy: literally “eating one’s brother”), as well as oophagy in odontaspid (sand tiger) and lamnid sharks, and limited matrotrophy by placenta-like maternal-fetal connections in many viviparous rays. Also included is likely oophagy by developing embryos (Boehlert et al., 1986) in the more K-selected *Sebastes* spp. Syngnathid pipefishes and seahorses (eight California species) brood embryos within or on their bodies and likely contribute substantially to their nutrition; the syngnathid reproductive mode, however, represents post-zygotic paternal care, not viviparity.

The time frame of maternal provisioning varies greatly among viviparous fishes. Gestation is typically several months long in the embiotocids (Baltz, 1984) and *Sebastes* spp. (Love et al., 1990) but is nearly 2 years long in the spiny dogfish (Jones and Geen, 1977).

Viviparity in California marine fishes would be almost entirely limited to elasmobranchs (and in that regard, unexceptional), were it not for the embiotocids (fig. 19-1A) and the sebastine genus *Sebastes* (fig. 19-1B). Because of these latter two groups, however, viviparity in California marine fishes is unusually well expressed. The embiotocids (20 marine species) plus *Sebastes* (nearly 70 species) comprise about 12% of all of the coastal shelf and slope fishes of the Californias (Miller and Lea, 1972; De la Cruz Aguero et al., 1997). Elasmobranchs comprise another 56 viviparous species. Including elasmobranchs, viviparous species total nearly 18% of the California marine fish fauna; this contrasts markedly with an overall value of less than 3% for marine elasmobranchs and teleosts worldwide (Wourms and Lombardi, 1992). Table 19-1 summarizes patterns of viviparity within and between both major groups of California marine fishes. Appendix 19-1 provides a more comprehensive list by (sub)family within order, with species examples and key references.

Parental provisioning of offspring often extends to parental care (guarding or brooding of eggs) in fishes. Post-oviposition (egg-laying) parental care is limited to teleosts in California as elsewhere. There are no known or likely cases of post-parturition parental care in viviparous elasmobranchs, although there are several well-documented cases (e.g., the soupfin shark, *Galeorhinus galeus*: Ripley, 1946) of sexual segregation in schooling species of viviparous sharks, presumably as a female adaptation to reduce predation of post-partum young by males. The types of teleost parental investment include the physiological nurturing and anti-predator defense of eggs (typically attached to some substrate, many California species) and sessile larvae (described for one California batrachoidid toadfish, the plainfin midshipman *Porichthys notatus*

TABLE 19-1

Contrasts Between Latitudes and Oceans in Reproductive Modes

(A) Viviparity				
Subclass	California	Pacific Canada	Atlantic USA	Atlantic Canada
Elasmobranchs	81.0 (79)	68.0 (19)	85.5 (76)	55.6 (36)
Teleosts	10.3 (798)	15.0 (301)	0.3 (1232)	0.6 (492)
(B) Teleost Parental Care				
Taxon level	California	Pacific Canada	Atlantic USA	Atlantic Canada
Species	15.5 (798)	19.3 (301)	16.9 (1232)	7.9 (492)
Families	15.5 (161)	22.5 (80)	13.4 (186)	8.5 (142)

NOTE: In A the proportional presence of viviparity (as percentage) is compared among species of California marine elasmobranch and teleost fishes. In B the presence of post-zygotic parental care (as percentage) is compared among oviparous species and families of California marine teleosts. Sources: Miller and Lea, 1972; De La Cruz Aguero et al., 1997; Fitch and Lavenberg, 1968; see Appendix 19-1 for complete listing. Also provided are comparative data for marine fishes of the Pacific (Hart, 1973) and Atlantic (Scott and Scott, 1988) coasts of Canada and the Atlantic USA excluding the Gulf of Mexico (Robins et al., 1986). Atlantic USA data for Alepocephalidae and Moridae are supplemented by Haedrich and Merrett (1988). Numbers in parentheses indicate total number of taxa.

[fig. 19-2], and likely for its congener the specklefin midshipman *P. myriaster*). Care of embryos or mouth-brooded fry (young juveniles) is undocumented for native California fishes, but the former is likely for the ariid catfishes *Arius planiceps*, *A. platypogon*, and *Bagre panamensis*, and the jawfish, *Opistognathus punctatus*. Oral-brooding males of the Guadalupe cardinalfish *Apogon guadalupensis* have recently been observed at San Clemente Island (Lea and Rosenblatt, 2000). Care of free-swimming fry is unknown and unlikely in native California fishes, although the triggerfish *Balistes polylepis* has been observed in the Gulf of California guarding free-swimming fry after swim-up from tended demersal spawn (Strand, 1978 and pers. comm. in Barlow, 1981). The introduced euryhaline cichlids *Oreochromis mossambicus* and *Tilapia zillii* (Knaggs, 1977) also brood both eggs and free-swimming fry (El-Zarka, 1956; Loiselle, 1977).

Parental tending of demersal eggs is the most prevalent form of care in California marine teleosts. About 16% of the species and over 15% of the families of oviparous California teleosts tend demersal eggs after oviposition (table 19-1). Although not unique to the Californias or the Pacific coast of North America, oviparous fishes that provide some sort of post-zygotic parental care of eggs are noteworthy for their divergent lineages as well as species diversity among the California and eastern north Pacific ichthyofauna. The presently recognized 43 species of California marine cottids and cottoids (Rhamphocottidae, Hemitripteridae) are the second most diverse lineage of California marine fishes, and many genera and species of cottids exhibit parental care. Parental care is apparently ubiquitous in the Hexagrammidae and is present in at least some Liparidae. Care is the norm in the gobioids and throughout the zoarcoid, blennioid, and gobiesocoid perciforms (Anarhichadidae, Blenniidae, Chaenopsidae, Gobiesocidae, Labrisomidae, Pholididae, Stichaeidae, Tripterygiidae). Parental care would not be unexpected in the Scytalinidae, Cryptacanthodidae, and Zoarcidae, the latter based on observations of species elsewhere, although care has thus far been anecdotally noted for only one species of California zoarcid (Levings, 1969). Most cases of care in native California marine fishes are paternal although a minority of exclusively maternal (one species—the triggerfish *Balistes polylepis*: Strand, 1978); biparental (the gunnels *Pholis laeta*: Hughes, 1986; and *Apodichthys flavidus*: Wilkie, 1966; the wolf-eel *Anarhichthys ocellatus*: Marliave, 1987); and maternal and facultatively biparental (the red Irish lord cottid *Hemilepidotus hemilepidotus*: Fig. 19-3; DeMartini and Patten, 1979) care states are known. One western North Pacific species of the cottid genus *Hemilepidotus* is also known to exhibit facultative biparental care (Hayakawa and Munehara, 1996). Care can include some type of physiological nurturing (fanning eggs to enhance gas exchange, developmental rate, and survivorship: buffalo sculpin *Enophrys bison*: DeMartini, 1978b; lingcod *Ophiodon elongatus*: Giorgi and Congleton, 1984), passive to active defense of eggs against conspecific and extraspecific predators (many species, including the painted greenling *Oxylebius pictus*: DeMartini, 1987), or both (DeMartini, 1999). Protective functions appear most widespread based on taxonomic prevalence (Coleman, 1999).

Overall, 32% and 26% of species and families, respectively, of all California marine fishes (elasmobranchs plus teleosts) are either viviparous or oviparous and exhibit parental care. The total proportion of viviparous and egg-tending species (36%) and families (34%) is even greater in the waters off Pacific Canada. In comparison, the marine fish faunas of both Atlantic USA and Atlantic Canada include relatively few viviparous and egg-tending species and families (2 × 4 chi-square tests: $P < 0.0001$; table 19-1A, B). The lack of increase with latitude in proportion of parental-caring teleosts in the western North Atlantic (table 19-1B) argues against a simple latitudinal explanation. Several families of viviparous or predominantly to exclusively parental-caring fishes are either conspicuously absent (embiotocids, hexagrammids) or comprise few species (sebastine scorpaenids, cottids) on the Atlantic seaboard. Table 19-1B also summarizes parental care patterns among families of California marine fishes, and a complete listing of parental care in California fishes is provided in Appendix 19-1. To our knowledge, ours is the first explicit documentation of the unusual preponderance of viviparity and parental care in California marine fishes. Kendall (1981) and Hobson (1994) were among the first to note the prevalence of parental-caring demersal spawners among eastern North Pacific fishes.

Care in some cases involves alloparental (genetically unrelated) adult conspecifics, other fish species, and associations with benthic invertebrates. Evaluation of alloparental care is deferred to a later section on mating systems and sexual selection. There is one known eastern Pacific example of extraspecific reproductive association among fishes (akin to some described associations of cyprinids spawning in the nests of centrarchids in North American freshwater systems—see review by Johnston,

FIGURE 19-2 Parental male of the plainfin midshipman, *Porichthys notatus,* placed upon an overturned, intertidal rock with a mass of large-yolky eggs. Midshipman males tend eggs layed by females on the underside of rocks in intertidal and subtidal areas. Photo by M.H. Horn.

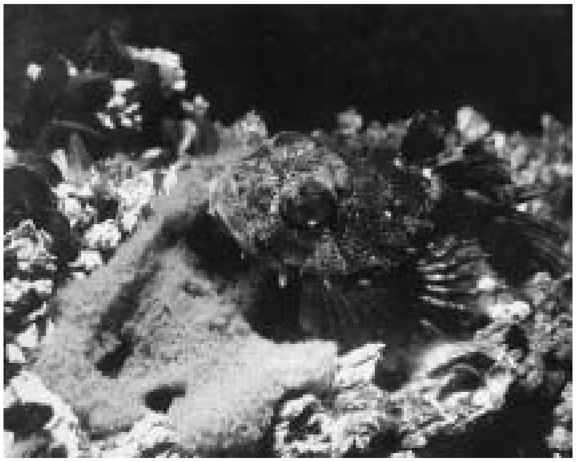

FIGURE 19-3 Parental female of the sculpin *Hemilepidotus hemilepidotus* reclining atop mass of demersal spawn. *H. hemilepidotus* is an atypical cottid (perhaps representative of the subfamily Hemilepidotinae) which exhibits primarily maternal and facultatively biparental guarding of spawn (from DeMartini and Patten, 1979 with permission from the Royal British Columbia Museum).

1994). The small-bodied sculpin *Asemichthys taylori* spawns its eggs on the surface of much larger egg masses tended by males of another cottid, the relatively large-bodied buffalo sculpin. Both sexes of *A. taylori* desert after spawning, and the association may represent a parasitism if peripheral spawns of the small species hinder gas exchange, developmental rate, or survival of the larger species' spawn (Kent et al., 1997). The association is at least as likely to be a commensalism whereby the small species alone benefits from the larger species' spawn defense without appreciable cost to the latter. One other case of extraspecific egg tending has been recently described, involving two species of freshwater cottids in Lake Baikal, which might represent interspecific competition for spawning sites, the acquisition of subordinate species' eggs by the dominant species for consumption while tending its own eggs, or both (Munehara et al., 2002). These and other possible sculpin nesting associations need further study.

Many demersal spawners lay eggs attached to algae or benthic invertebrates; in many cases eggs are hidden within benthic fouling organisms (DeMartini, 1999). Many species of aparental northeastern Pacific sculpins, for example, deposit spawns in places inaccessible to predators within rock crevices and kelp holdfasts or among barnacle tests and mussel valves. Some species, like the silverspotted sculpin *Blepsias cirrhosus*, sequester eggs within sponges and perhaps benefit from the chemical defense afforded by sponge toxins as well as by physical protection and ventilation within the sponge structure (Munehara, 1991). Some liparid snailfishes of the genus *Careproctus* have evolved yet another unique invertebrate association: females deposit eggs within the gill chambers of lithodid crabs, and embryos benefit from enhanced ventilation as well as physical protection in a parasitic relationship with a survivorship cost to the crab host (Somerton and Donaldson, 1998).

The numerous and diverse examples of post-zygotic parental care in oviparous species and viviparity represent a suite of adaptations for improving offspring survival; such adaptations are likely antipredatory because of the dominant influence of predation in marine ecosystems (Valiela, 1995). Without the pervasive influence of predation countering offspring survival, the present variety of investment patterns and related parental care systems in California marine fishes surely would be much less developed. We next briefly review key issues in the reproductive life histories of fishes and provide California examples as prelude to a discussion of courtship behaviors and other aspects of the behavioral and evolutionary ecology of reproduction in these fishes.

Key Attributes of Reproductive Life Histories

Optimizing offspring production inevitably leads to tradeoffs between the number versus size of offspring ("many small versus few large"; Winemiller and Rose, 1992b) and to the evolution of adaptations which both augment investment in individual offspring while maximizing the numbers of offspring produced (Elgar, 1990). The former includes traits that enhance the survival of individual propagules after parturition or oviposition—greater maternal investment per offspring (larger eggs, viviparity) and parental care after egg-laying. The latter includes the production of multiple broods in both egg-layers and live-bearers.

Adaptations that maximize offspring production in California marine fishes, and fishes in general elsewhere, are centered on rates of egg production by females. Even though seasonal productivity cycles influence the timing of reproduction, the females of many if not most species of oviparous teleosts, in California and other temperate marine ecosystems, ripen and spawn multiple clutches of eggs over a protracted reproductive period and repeat this process over many years once sexual maturity has been attained. Numerous case studies (e.g., DeMartini, 1991) illustrate how annual per capita offspring allocation is increased through multiple spawning events. As a consequence, gonadal investment is typically severalfold larger than somatic production in adult fishes (DeMartini et al., 1994). Some of the more *r*-selected species of viviparous *Sebastes* in California (Moser, 1967; Love et al., 1990), like both freshwater live-bearers (guppies, F. Poeciliidae) and some marine live-bearers elsewhere (viviparous Australian [Gunn and Thresher, 1991] and South African [Prochazka, 1994] clinids), have evolved the analogous process of superfoetation (the live-bearing of multiple broods whose embryos are produced in partially overlapping series). Superfoetation has not evolved in any embiotocid (Baltz, 1984). Perhaps superfoetation to some extent augments offspring number at the expense of offspring size and any reduction in offspring size would oppose this major selective factor favoring the maintenance of viviparity in the group. Or, perhaps the restricted seasonal timing of offspring production in embiotocids precludes superfoetation, given the recognized importance of brood timing among females of differing sizes and ages in one species (Schultz et al., 1991).

Fishes, being the most primitive and developmentally plastic of the vertebrates (Francis, 1992), have the further capability of adjusting reproductive effort by flexible gender allocation (Warner, 1978). That is, it is within the evolutionary scope of teleost fishes for individuals to not only change sex ontogenetically (sequential hermaphroditism) but to concurrently maintain both egg as well as sperm-producing capabilities (simultaneous hermaphroditism). In the two basic types of sequential sex change—changing from adult male to adult female (protandry) or from female to male (protogyny)—the sexes are dioecious (separate) and individuals do not function as both sexes at the same time. A local example of a protogynous teleost is the California sheephead *Semicossyphus pulcher* (Warner, 1975a).

Some dioecious species have evolved more than one morphotype of one of the sexes (e.g., diandry involving two male types: Reinboth, 1970). In sex-changing species, multiple morphs typically occur only in the nonlimiting, usually male, sex. Diandry has been most frequently described in protogynous wrasses of the Labridae. It has been widely theorized but rarely demonstrated that the proportion of the different morphs in reproducing population units is dynamic and subject to frequency-dependent selection such as might occur under different population densities. The evolution of multiple within-sex morphs has not been limited to sex-changing species, however. California marine examples include the jack and hooknose males of salmonids like *Oncorhynchus kisutch* (Healey and Prince, 1988), and the so-called Types I and II males of the plainfin midshipman (Brantley and Bass, 1994; Barni et al., 2001). Other well-studied examples of satellite and sneaker males (subordinates that use deceptive tactics to counter the defense of females or spawning sites by dominant males) include freshwater sunfishes like bluegill *Lepomis macrochirus* (Gross, 1982) and bluehead wrasse *Thalassoma bifasciatum* (a sex-changing species) of Caribbean coral reefs (Warner and Schultz, 1992).

In monoecious (simultaneous) hermaphrodites, individuals can perform both sexual functions at the same time. Many deep-sea fishes throughout the world's oceans are monoecious hermaphrodites (Mead, 1960; Mead et al., 1964; Smith and Atz, 1973; Fishelson and Galil, 2001). It is likely that simultaneous hermaphroditism has provided a solution to the general problem of locating sparsely distributed mates (Tomlinson, 1966) in diverse lineages of deep-sea fishes (Smith, 1975). Functional rather than anatomical hermaphroditism has been another solution for deep-sea fishes. The most extreme examples of the latter are the deep-sea ceratioids, in particular ceratiids such as *Cryptopsaras couesii*, in which tiny males once having encountered a female, become little more than ectoparasitic testes on females' bodies (Pietsch, 1976). Among nearshore California fishes, examples of simultaneous hermaphrodites include gobies of the genus *Lythrypnus*. In bluebanded (*L. dalli*) and zebra (*L. zebra*) gobies, the proportion of gonad allocated to the two sexual functions is variable and dynamic, dependent on diverse aspects of the social environment including the relative body sizes, density, behavioral gender, and spatial distributions of conspecifics (St. Mary, 1993, 2000). Studies of the complex interplay between the social environment and the neuroendocrine bases of sex change have been conducted for the bluebanded goby (Reavis and Grober, 1999; Carlisle et al., 2000) and for California sheephead and rock wrasse *Halichoeres semicinctus* (Diener, 1976).

Maximizing fitness in some cases appears to have selected for multiple types of gender allocation within populations. Populations of the bluebanded goby for example contain sequential hermaphrodites (protogynous pure males) as well as simultaneous hermaphrodites (St. Mary, 2000). Simultaneous hermaphroditism and bidirectional sex change (either from mature female to mature male, or vice versa) are known to occur in several genera of tropical gobiids, but as yet both have not been described within the same species-population (Kuwamura et al., 1994; Nakashima et al., 1995, 1996). Mixtures of protogynous and gonochoric (non-sex changing) individuals occur in populations of a warm-temperate serranine (the spotted sand bass *Paralabrax maculatofasciatus*) in Baja and southern California (Hovey and Allen, 2000). Populations of several tropical serranines (e.g., *Serranus psittacinus* = *S. fasciatus* of Hastings and Petersen, 1986; Petersen, 1990a) also simultaneously include hermaphroditic and protogynous individuals. Gender allocation patterns exhibited by families of California marine fishes are summarized in tables 19-2 and 19-3 and catalogued in greater detail in Appendix 19-1. The most likely selective agents favoring the evolution of hermaphroditism in fishes are discussed in the third section.

Fitness is influenced by the per capita survival of offspring after oviposition or parturition. Larger propagules have higher survivorship (Ware, 1975; Pepin, 1991; Wootton, 1994), so selection for greater energetic investment per offspring occurs coincident with selection to produce greater numbers of offspring. This is why, within-species, larger-bodied females, which are both capable of (having a greater body cavity volume) and selected for (being generally older and consequently of lower reproductive value) allocating a larger proportion of their available energy to reproduction, typically compromise between producing more and larger offspring. As predicted by optimization theory (Chambers and Leggett, 1996), the larger-bodied, older females of many species of California marine fishes produce larger, as well as more numerous eggs (e.g., *Engraulis mordax*: Parrish et al., 1986; *Seriphus politus*: DeMartini, 1991). The eggs produced by pelagic spawners average smaller in size than those produced by demersal spawning fishes (Duarte and Alcaraz, 1989); brooded eggs in general tend to be larger than untended demersal eggs (Sargent et al., 1987; Winemiller and Rose, 1992a); and the embryos of larger eggs hatch as larger larvae (Chambers and Leggett, 1996). Viviparity and post-zygotic parental care to some extent involve increased investment per offspring (hence larger individual offspring) at the expense of the numbers of offspring in which the total investment is made. Selection for the production of relatively few but large offspring has been disproportionately frequent in the marine fishes of California and the Pacific coast of North America. In Section IV we will discuss some likely reasons why this has come about.

Courtship

Courtship behavior and the events that often accompany it has been a favorite topic among lay persons and field biologists alike. In part this is probably because such acts contrast strongly with the background of normal behavior. While many aspects of reproductive ecology can be inferred from surveys (e.g., paternal care can be assessed by the presence of males guarding eggs, which may last weeks) or collection of

TABLE 19-2

Shallow-Water Marine Fish Families with One or More Species Having Known or Likely Non-Gonochoric Gender Allocation

Teleost Family	*Type(s) of gender Allocation*	*California Representation?*
Muraenidae	protogynous, protandrous, simultaneous, gonochoric	yes; lone sp. likely gonochoric
Caracanthidae	protogynous	no
Platycephalidae	protogynous, gonochoric	no
Centropomidae	protandrous	no
Serranidae	simultaneous, protogynous, gonochoric	yes; all three types likely
Malacanthidae	protogynous, gonochoric	yes; lone sp either one or other type
Sparidae	protogynous, protandrous	yes; lone sp likely protogynous
Lethrinidae	protogynous	no
Nemipteridae	protogynous, gonochoric	no
Polynemidae	protandrous	yes; both spp likely protandrous
Cirrhitidae	protogynous, bidirectional	no
Pomacentridae	protandrous, protogynous, gonochoric	yes; all spp gonochoric
Labridae	protogynous, gonochoric	yes; both types represented
Scaridae	protogynous, gonochoric	yes; lone expatriate sp likely protogynous
Trichonotidae	protogynous	no
Creediidae	protandrous, gonochoric	no
Gobiidae	protogynous, simultaneous, bidirectional	yes; all three types represented
Ostraciidae	protogynous	no

NOTE: List of 18 families excludes those in the deep sea. A subset representing California marine fishes is provided for comparison. Additional details are listed in Appendix 19-1.

TABLE 19-3

Proportional Distribution of Gender Allocation Among Reef and Other Inshore Teleosts of California Versus the Tropics

	California	*Tropics*
Gender Allocation Type	*Percentage (N Families)*	*Percentage (N Families)*
gonochore	87.2 (34)	67.1 (53)
protogynous hermaphrodite	10.3 (4)	21.5 (17)
protandrous hermaphrodite	0	7.6 (6)
sequential or bidirectional hermaphrodite	2.5(1)	3.8 (3)
total hermaphrodites	12.8 (39)	32.9 (26)

NOTE: Tropical families include Indo-Pacific, Caribbean, and Atlantic. Numbers of allocations for families outnumber families due to multiple allocation types within some families like the Serranidae and Gobiidae.

individuals (e.g., sex change), details of courtship and spawning require direct observation in the right place at the right time. Thus, data are biased toward species that are most easily observed and for which spawning is most predictable in time and space. For purposes of this review, we define courtship as a form of communication that increases the likelihood of the receiver spawning or copulating with, and thus benefiting, the sender (e.g., Myrberg and Fuiman, 2002). For an excellent review of communication in animals generally, including courtship, we refer the reader to Bradbury and Vehrencamp (1998).

In fishes, courtship may involve impressive visual displays such as rapid body movements and conspicuous changes in coloration and sounds, often easily detectable by unaided human observers, along with chemical and electrical signals that are not detectable by the unaided observer. Courtship per se is a sexually selected trait that is usually associated with males, ostensibly because males are more often the limited sex. However, courtship behavior has been described for females of many fish species as well, perhaps most notably in syngnathids where males are often the limiting sex (e.g., Gronell, 1984; Berglund and Rosenqvist, 2001). Courtship activity in fishes and other organisms appears to have at least four functions. The simplest and most obvious of these is species identification and an indication of individual reproductive state. Courtship may also help synchronize the release of gametes. This would seem to be particularly important in pair or group-spawning species that release gametes directly into the water column.

Courtship may provide information about the quality of the individual or the spawning site. For example, female bicolor damselfish (*Stegastes partitus*) spawn preferentially with males that court more vigorously and more vigorous courtship is correlated with both male fat reserves and hatching success of the eggs guarded by parental males (Schmale, 1981; Knapp and Kovach, 1991). In the bluehead wrasse, aspects of male courtship are influenced by the presence of piscivores known to feed on spawning adults and thus courtship display can provide information about the safety of the spawning site (Warner and Dill, 2000). In some three-spined stickleback (*Gasterosteus aculeatus*) populations the intensity of red coloration may be a reliable indicator of male parasite loads

(Milinski and Bakker, 1990). The function of courtship, or a given component of courtship, in a given species likely depends on its spawning mode and mating system, and courtship and spawning behavior can be expected to reflect and respond to the tradeoffs between maximizing the benefits of courtship favored by sexual selection (increasing reproductive success), relative to their costs (e.g., energy expenditure, predation on adults or offspring, opportunity costs).

Research on courtship in fishes, as in other organisms, has focused on the full range of levels of inquiry, including proximate/physiological mechanisms (e.g., Stacey, 1987; Bass, 1993), the evolutionary history of courtship signals (Basolo, 1990a; Foster, 1994), and the function of courtship signals. However, as with other types of behavior, most research on courtship and spawning behavior in temperate marine fishes, including those off the coast of California and adjacent waters, has not progressed beyond the descriptive phase, often coming from opportunistic observations, and has focused on relatively few species. Below we summarize descriptive studies of courtship and spawning behavior in these species as well as the few studies that have gone beyond the descriptive phase.

Of the range of spawning modes and reproductive tactics found in marine fishes off the coast of California, details of courtship and spawning are probably best documented for fishes in which males defend reproductive territories. These include species with internal fertilization and no subsequent male care (e.g., some *Sebastes* and Cottidae), but especially those in which male territories include egg-deposition sites. This bias exists despite the fact that reproductive territoriality remains poorly documented (discussed below), probably because the site, and often the timing, of reproduction are predictable: Male reproductive territories are easily identified by conspicuous male behavior and/or the location of a nest site. Thus, by remaining at that site, a patient observer is likely to witness courtship and spawning. Of course, patience wears thin in the cold waters of the temperate eastern Pacific and most of the work has still focused on a small number of common, conspicuous, and shallow-water species, much of it under laboratory conditions. Moreover, in many field studies, observations have been opportunistic and courtship was inferred from the location of the interaction and the sex and reproductive status of interacting individuals, rather than observations of events actually culminating in spawning or copulation. In addition to Tinbergen's (1952) classic description for sticklebacks, Myrberg (1972), Losey (1976), and Munehara (1988) provide good examples and detailed ethograms of typical courtship behavior in male-territorial species.

Where males guard egg-deposition sites or mating territories that do not include females (as occurs in haremic species which defend access to members of the opposite sex), males must attract females to their territory in order to spawn or copulate. Similarly, ripe females must have the opportunity to enter the territory and assess the quality of prospective mates, rather than being evicted as an intruder or ignored, and thus must at least advertise their gender, if not their reproductive status. This would appear to favor displays that increase male conspicuousness against the visual, auditory and/or chemical background of the environment, while inhibiting or concealing territorial keep out signals, and female displays that are reliable indicators of female fecundity and readiness. The types of signals used should reflect the resolution of the tradeoff between the specific costs and benefits of signaling and mate-visiting for each sex, local or species-average environmental variables that affect signal detectability, and phylogenetic constraints. Costs of courting for territorial males include increased conspicuousness to predators or other males (e.g., sneak spawners), and energy expenditure. Predation risk is also a potential cost for females, whose often swollen abdomen may both increase conspicuousness and reduce swimming efficiency. For both sexes, these costs should be affected by body size and morphology that affect susceptibility to predators and swimming efficiency. If males leave the territory to court, they further risk injury from other territorial fishes, losing eggs to predators, and territorial resources (or the entire territory) to competitors. Females that occupy territories similarly risk losing resources to competitors (Karino and Kuwamura, 1997; Sikkel, 1998) and risk injury when crossing territories of other fish (Reynolds and Côté, 1995). One perhaps counterintuitive cost of courtship for males in nest-guarding species is that females, attracted to the nest, are often themselves egg-predators (e.g., Foster, 1990; Fitzgerald, 1991; Sikkel, 1994b). In males, courtship activities that reduce costs for females may be favored even if (or possibly because) they are costly for males. For example, female travel costs may be offset by increasing the conspicuousness of the signal, making it easier for females to locate the territory, or by courting females in their own territories and leading them to the spawning site, as occurs in many damselfish species (Karino, 1995).

Numerous examples demonstrate the effects of the costs and/or benefits of courtship mentioned above on different components of courtship and mating in fishes (e.g., Reynolds, 1993; Godin and Briggs, 1996; Foster 1994). Among male-territorial species represented in California, male garibaldi (*Hypsypops rubucundus*) (Fig. 19-4), painted greenling, and plainfin midshipman have been observed to decrease courtship when eggs are in an advanced stage of development (DeMartini, 1987, 1988b; Sikkel, 1989). Where it has been measured, this change in male behavior is associated with a decrease in plasma levels of androgens (Sikkel, 1993; Knapp et al., 1999). At least in the first two species, females virtually never spawn in such nests (low benefit to courtship) but may eat eggs (high cost to courtship). These patterns have also been well-documented for populations of three-spined sticklebacks (Rohwer, 1978) although they cannot be assumed to be universal given the high degree of among-population variation in behavior in this species (Bell and Foster, 1994). Courtship effort in nesting male garibaldi also appears to be sensitive to the quality of the nest, which similarly affects the probability of female spawning. Females prefer to spawn in nests with thicker algal growth, and males whose nest quality has been reduced decrease their courtship activity relative to controls (Sikkel, 1995a). Among territorial female garibaldi, those with higher apparent intruder pressure have shorter bouts of mate-sampling and thus visit fewer males per bout (Sikkel, 1998).

Visible elements of courtship displays in territory-guarding species include some combination of rapid body movements, including dips, loops, zig-zag swimming, lateral undulations, rapid swimming toward the nest (leading), opercular flaring, and conspicuous coloration. Coloration can be of two types: structural colors which are relatively permanent, and pigments, usually found in chromatophores, that can be differentially deposited into or expressed by their contraction or expansion within the chromatophores (e.g., Bagnara and Hadley, 1973; Endler, 1991).

One constraint imposed on the use of visual signals underwater is the differential absorption of light wavelengths with depth and limited horizontal visibility. The latter may be particularly problematic in coastal areas, especially above Point

FIGURE 19-4 Male of the garibaldi, *Hypsypops rubicundus* guarding its nest (right). From March-July, the male builds a nest on the reef. He cleans away all growth except for filamentous red turf algae and trims the nest into an oval about 50 cm in diameter. The male garibaldi displays near the nest and makes clicking noises to lure females. After entering, a female lays her eggs within the nest and the male fertilizes them externally. The eggs attach to the nest where the male aggressively guards them for up to two weeks at which time the larvae hatch and enter the plankton. Photo by P. C. Sikkel.

Conception, where the effects of upwelling are most prominent and visibility is reduced, and less so around the Channel Islands offshore of southern California. Thus, carotenoid-based pigmentation will only be visible in shallow water, and the effectiveness of any color, along with behavioral displays, will often only be effective over short distances.

Sex-specific coloration (sexual dichromatism) used in reproductive communication falls into three categories. First, dichromatism can be present year-round, with no change between spawning and nonspawning periods. Second, it can be seasonally permanent (always present during the spawning period) but disappear during the nonspawning period. Color differences may persist only during mate-visiting, pairing, or spawning. Selective forces other than reproduction that affect selection on background coloration will place constraints on the types of permanent or temporary sex-specific coloration, and in our ability to determine what, if any, role those colors play in courtship and mate choice. In many cases, coloration can serve more than one function. For example, color patterns used by males to attract females may simultaneously serve as warning signals directed at conspecific males (e.g., *Xiphophorus* swordtails: Morris et al., 1995; painted greenling: DeMartini, 1985). Moreover, some species exhibit considerable among-habitat color variation that represents differences in habitat use, rather than the influence of sexual selection. Finally, some fishes may detect light wavelengths, such as ultraviolet (McFarland and Loew, 1994; Losey et al., 1999), that are not perceived (and are thus ignored) by human investigators. Nevertheless, some studies have found evidence of a role of male-specific coloration and female mate choice in some male-territorial marine fishes (e.g., Warner and Schultz, 1992).

All types of reproductive coloration are represented among California's territorial or reef-associated marine fishes. Among the temperate reef fishes found off California's coast, highly conspicuous (at least to humans) coloration for either sex is extremely rare, unlike their tropical counterparts, and is limited to a few tropical derivatives usually found south of Point Conception. In three of these (the orange garibaldi damselfish, the blue and red bluebanded and zebra gobies), there is no apparent sexual dichromatism. In contrast, the large, male-territorial (Adreani et al., 2004) sheephead wrasse (fig. 19-5) is conspicuously dichromatic and dimorphic, and the smaller, also male-territorial rock wrasse less so (fig. 19-6). None of these species, except perhaps male rock wrasse (DeMartini, pers. obs.), exhibit seasonal or spawning-specific changes in coloration. Among the generally less conspicuous male territorial species, easily distinguishable permanent or seasonal dichromatism is also uncommon. Notable exceptions include two hexagrammids (kelp greenling *Hexagrammos decagrammus*; painted greenling: DeMartini, 1985, 1986; figs. 19-7 and 19-8), in which males and females occupy different microhabitats. Both of these species also exhibit additional sex-specific color patterns during courtship and spawning, which seems to be almost universal among the cryptically

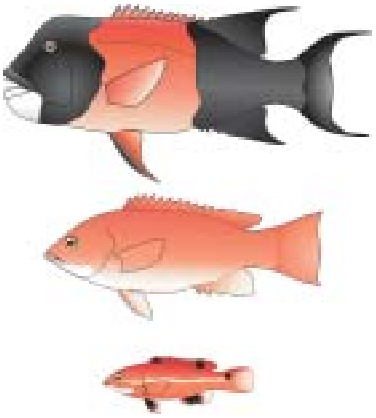

FIGURE 19-5 Terminal phase male (top), primary phase female (middle), and juvenile phase (bottom) California sheephead *Semicossyphus pulcher* (artwork by L. G. Allen).

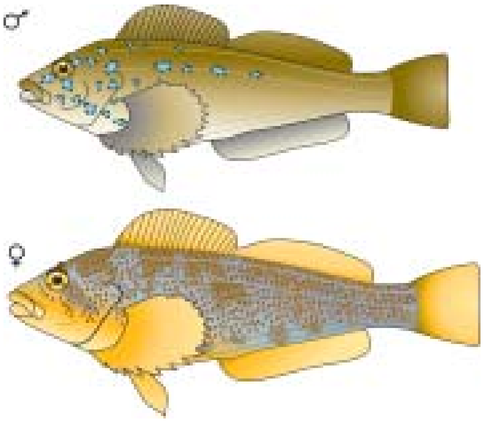

FIGURE 19-7 Male (top) and female (bottom) kelp greenling *Hexagrammos decagrammus*. Dark-blotched pattern appears on female only during courtship (artwork by L. G. Allen).

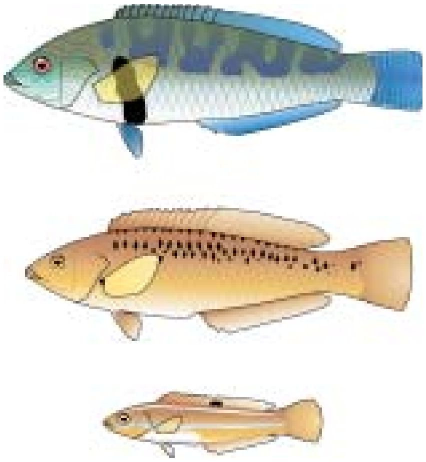

FIGURE 19-6 Terminal phase male (top), primary phase male/female (middle), and juvenile phase (bottom) rock wrasse *Halichoeres semicinctus* (artwork by L. G. Allen).

colored (see Eschmeyer et al., 1983) hexagrammids, scorpaenids, cottids, blenniids, and clinids that have been studied. Most commonly, the courtship-associated color patterns involve an overall or partial darkening or paling relative to their typical color pattern. In some species males and females intensify the sex-specificity of colors and patterns during courtship (e.g., pale head spots are emphasized and dark trunk speckles are suffused as blotches by male and female kelp greenling, respectively; pale spots on the head and trunk are contrasted against a deeply darkened background color by male painted greenling: fig. 19-8; DeMartini, 1985).

One of the more intriguing forms of courtship display that involves temporary color change is light produced by bioluminescent photophores. Although bioluminescent communication is found in some terrestrial organisms, it appears to be particularly common among nocturnal and deep-water marine organisms (Lloyd, 1977; Herring 2000). However, at the low densities often characteristic of some deep-sea fishes for which bioluminescence is thought to be important, it is unclear whether light can be seen at sufficient distances to serve as a primary attractant (Baird and Jumper, 1995; Herring, 2000). Instead, chemical or other factors may serve as the primary attractant, with bioluminescence functioning at closer distances. Among coastal California species, the use of photophores during courtship has been suggested for plainfin midshipman (Crane, 1965; Christophe and Baguet, 1985). However, in their detailed laboratory studies of courtship in this species, Brantley and Bass (1994) did not observe bioluminescence during courtship. Given the geographic variation in the expression of bioluminescence in this species, their observations may reflect a local anomaly. Clearly more work is needed to resolve the role of bioluminescence in courtship in this species.

The typical motor patterns described above that are performed during courtship appear to be visual signals; however, they may often be perceived instead or additionally through the acoustico-lateralis system or may provide a means of dispersing reproductive pheromones (Shinomiya and Ezaki, 1991). In many paternal-caring species, if the male is successful in attracting a female to the nest, he will often swim rapidly around and may even bite her until or even during spawning, and may also chase her from the nest before, during, or after spawning. However, it is unclear whether the female is being evicted from the nest or is being chased in response to her deviation from spawning-typical motor patterns or position, which could signal her intention to eat eggs. Among species found in the region covered by this review, courtship displays such as these have been observed in pomacentrids (Sikkel, 1988; Lott, 1995), clinids (Coyer, 1982), hexagrammids (DeMartini, 1985, 1986), gobiids (Cole, 1982), cottids (Munehara, 1988; Hayakawa and Munehara, 1996); and scorpaenids (Helvey, 1982; Shinomiya and Ezaki, 1991; Gingras et al., 1998).

Courtship-associated motor patterns, morphology, and color-changes also occur in females, perhaps most notably, but not solely, in those species in which males are frequently the limiting sex (e.g., syngnathids). Perhaps the simplest form of female visual display indicative of spawning-readiness, and potentially quality, is a swollen abdomen often associated with ripe eggs in the ovary. The best documented example of female courtship in paternal-caring fishes is the solicitation display of female threespine sticklebacks, which approach nesting males in a head-up posture, exposing their egg-

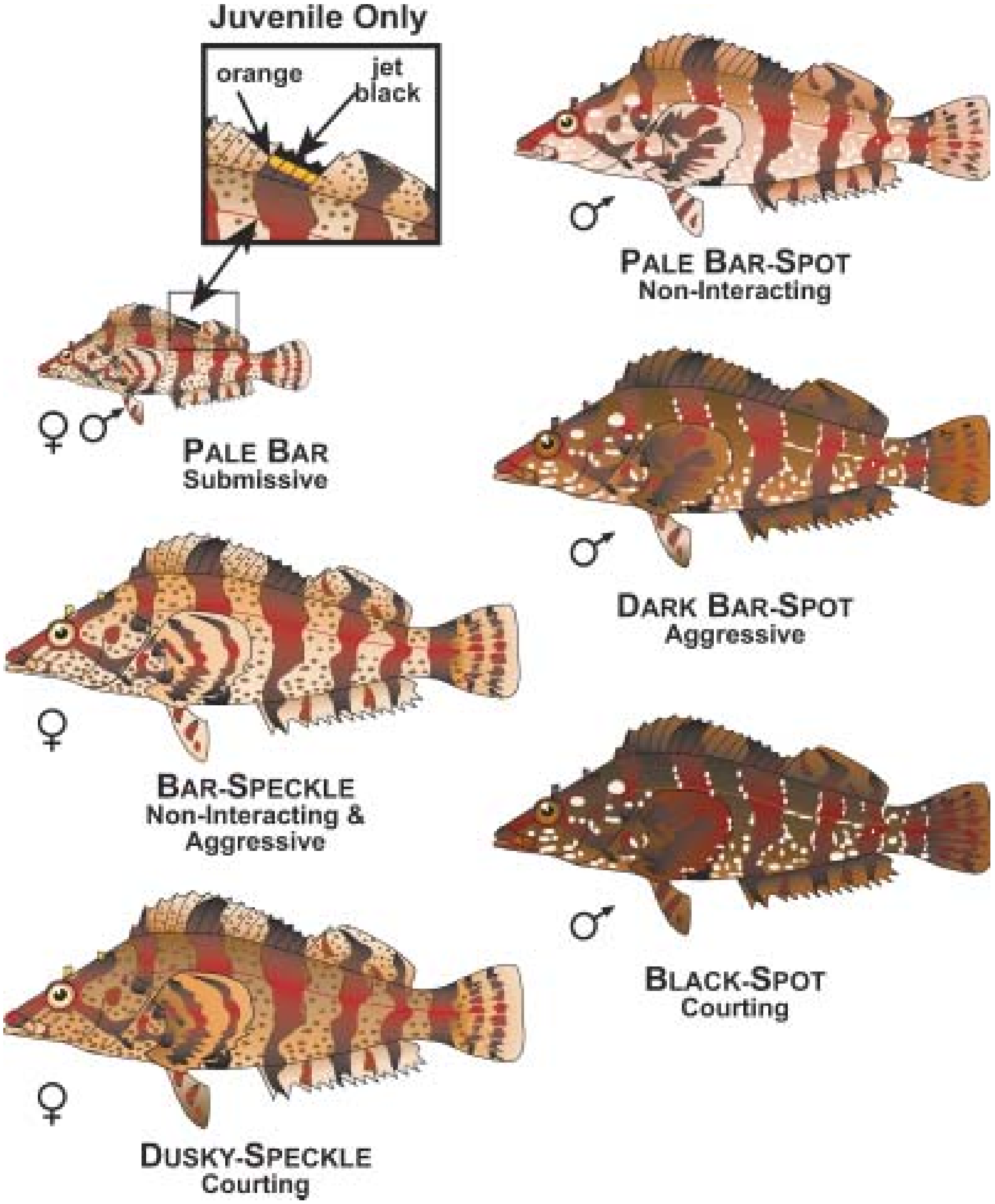

FIGURE 19-8 Juvenile (top left), adult female (mid and lower left), and adult male (top-bottom right) painted greenling *Oxylebius pictus* (after DeMartini, 1985 with permission from Allen Press).

swollen abdomen. The use of dummies to isolate the effects of morphological features from other, potentially confounding, effects of female behavior has shown that male courtship response is positively influenced by the head-up posture and size of the swollen abdomen (Rowland 1982, 1989, 1994; Bakker and Rowland, 1995).

More recently, the effect has been shown to be strongest when models are shaped to include the lordosis posture exhibited by females with the highest degree of spawning readiness (Rowland et al., 2002). However, visible (to the human observer) swelling or lordosis does not appear to be universal in fishes. In garibaldi, females searching for males do not appear obviously swollen but erect their median and pelvic fins and swim with exaggerated lateral undulations. Males court a female that swims in such a manner but when she retracts her fins and resumes swimming in a normal fashion, she is ignored or chased (Sikkel, 1988). Female painted greenling similarly exhibit stereotyped swimming movements a meter above the substratum, associated with a distinctive color change when approaching territories of nesting males who subsequently court them (DeMartini, 1985), and female *Hypsoblennius* exhibit a distinctive color change along with a submissive posture when approaching male nests (Losey, 1976). As with males, temporary color changes in females typically involve an overall or partial darkening or paling, relative to typical background coloration and to male coloration.

Acoustic signals associated with courtship occur in a wide range of fishes, and, where males defend reproductive territories, are typically performed by males (e.g., Myrberg, 1972; Hawkins, 1993). Sounds have also been recorded during spawning itself (e.g., Lobel, 1992; Lobel and Mann, 1995). Muscular squeezing of the swimbladder often produces sounds, and some species rapidly chatter the pharyngeal teeth (Rice and Lobel, 2002). To our knowledge, courtship sounds have been reported for only two male-territorial species found off California's coast: garibaldi and midshipman toadfishes. However, it is likely that use of acoustic signals during courtship, much of it inaudible to human observers, is quite common. For example, while acoustic courtship signals are unknown for California's gobies, drumming and tonal sounds, which appear to be produced by contraction of the swimbladder, have been recorded for nesting males of other goby species in the presence of females (Tavolga, 1958a; Lugli et al., 1995). Courtship sounds have also been reported in male blennies (Tavolga, 1958b). The gasbladder musculature of *Sebastes* rockfishes is indicative of a sound-producing function (Hallacher, 1974) although no studies have described the use of sound during courtship in this genus.

Like many other pomacentrids (e.g., Myrberg, 1972), male garibaldi produce loud chirping or thumping sounds during signal jumping displays, when leading females to the nest, and occasionally while spawning (Sikkel, 1988). Because they occur simultaneously, it is difficult to decouple the function or effect of sound versus the visual component of the display. However, females of at least some species respond to recorded courtship sound, independent of the presence of a courting male, and only during the spawning period and when their eggs are ripe (Mohler, 1984; Myrberg et al., 1986). This suggests that sound at least can have an independent effect. Unique sounds associated with spawning itself have also been reported in pomacentrids (Lobel and Mann, 1995). The mechanism of sound production in pomacentrids is still uncertain.

Whether sounds produced by garibaldi convey information aside from the male's location, reproductive state, and likely species identity is unknown. Acoustically based species and even individual recognition have been reported in some pomacentrids (Myrberg and Spires, 1972; Myrberg et al., 1978; Spanier, 1979; Myrberg and Riggio, 1985), and sound is also a reliable indicator of male size, with larger males producing lower frequency sounds (Myrberg et al., 1993; Lobel and Mann, 1995).

Among the best documented examples of auditory courtship signals in fishes are the batrachoidid toadfishes (e.g., Gray and Winn, 1961), including the nocturnally spawning plainfin midshipman (Ibara et al., 1983). Although both Type I (nesting) and Type II (sneaking) male midshipman, as well as females, are capable of producing grunts, used in agonistic interactions, only nesting males produce the long-duration (up to 14 min) hums, which can be heard over many kilometers during the spring-summer spawning period. Type I males are much larger and have a sixfold larger sonic muscle than do Type II males (Brantley and Bass, 1994). Nest-guarding Type I males begin humming shortly after dusk. Under laboratory conditions, ripe females appear excited when in the presence of a humming male and orient toward the source of the sound. The fundamental frequency of the hum is temperature dependent (Brantley and Bass, 1994). Again however, whether sufficient among-male variation in hum characteristics exists and whether it is used by females during mate choice is unclear: captive females attracted to nests of humming males spawned or exited the nest without spawning in approximately equal proportion, suggestive of female discrimination among males.

The release of water borne molecules that affect the reproductive behavior of conspecifics and thereby act as reproductive pheromones has been reported for males and females of some fish species. Many, perhaps most, of these pheromones appear to be steroid hormones, prostaglandins, or their metabolites that leak from or are excreted by the fish and thus can be used to convey information about the reproductive status and possible quality of individuals. Such hormonal pheromones can affect same and/or opposite sex conspecifics and can have either priming or releasing effects on the receiver. For recent, thorough reviews on the role of hormonal pheromones in fish reproduction, see Sorensen and Stacey (1999), and Stacey and Sorensen (2002). Evidence for hormonal or other reproductive pheromones has been found in over 100 species that include six orders found off California and adjacent waters (Clupeiformes, Osmeriformes, Salmoniformes, Scorpaeniformes, Perciformes, and Petromyzontiformes). Interestingly, in the latter (lampreys), a bile steroid appears to serve as the sexual attractant (Li et al., 2002). Thus, it seems likely that the use of pheromones in at least some aspects of courtship and spawning in reproductively territorial fishes off California is widespread. Direct or circumstantial evidence of the production of pheromones that affect female reproductive behavior has been reported for males of at least seven fish families that include California residents, although to our knowledge this list does not specifically include members that are found off California's coast.

Among the earliest documented indications of male courtship pheromones comes from studies on nesting male gobiids (Tavolga, 1956), which also provided the first evidence of the use of hormone-derived pheromones for courtship in male fishes (Colombo et al., 1980). In many gobies, males possess a specialized testicular gland (Miller, 1984). This gland contains high concentrations of Leydig cells that produce androgen conjugates that appear to attract and stimulate ovoposition in females of at least one species (*Gobius niger = G. jozo* of Columbo et al., 1980), and evidence of physiological response to both conjugated and unconjugated steroids has been found in another goby (Murphy et al., 2001; Murphy and Stacey, 2002).

Male reproductive pheromones also occur in nest-guarding cottids (Dmitrieva et al., 1988) and blenniids, the latter including at least one species (*Salaria pavo*) that appears to possess a specialized organ for pheromone production (Stacey et al., 1986; Zeeck and Ide, 1996; Oliveira et al., 2001). Losey (1969) described the release of pheromones produced by males of the genus *Hypsoblennius* that included two species found off California. However, these pheromones, produced by courting and spawning males, appeared to attract other males and not females. Territorial male *Sebastes inermis* and *S. miniatus* (not a confirmed male-territorial species) direct their urogenital region toward the head of females during courtship, suggesting release of a pheromone (Shinomiya and Ezaki, 1991; Gingras et al., 1998).

Release of reproductive pheromones appears to be much more common in females, even among male-territorial species (Stacey, 1987). Tavolga's (1956) classic work on *Bathygobius soporator* included the demonstration of a female pheromone that triggers courtship in males. Similarly, exposure to water from peri-ovulatory females increases courtship rates by male blackeye gobies (*Rhinogobiops* = *Coryphopterus nicholsi*) compared to water from empty tanks or water from non peri-ovulatory females (P. Sikkel and B. Shoplock, unpubl. data). In paternal-caring species where male courtship and female spawning site choice appear to be affected by egg developmental stage, the proximate causes are not well understood. Given the widespread occurrence of reproductive pheromones released by adults, the release of inhibitory or stimulatory compounds from the eggs themselves is an intriguing possibility.

In species that live or spawn in aggregations or schools, or in which males are haremic and thus control access to females, prospective mates are usually in close proximity and thus the challenge of attracting or locating a mate is greatly simplified. However, in all cases in which fertilization is external and gametes are released into the water column, spawning must be highly synchronized, especially when spawning occurs in pairs. As in other organisms, this can be accomplished by some combination of tactile, visual, olfactory, and auditory cues. For example, male nudging of the female's abdomen is an extremely common prelude to spawning ascent in many reef fishes (Thresher, 1984), and sound production associated with the spawning rush has been reported in some (Lobel, 1992). In captive studies, Hovey (2001, unpublished data) reported temporary sex-specific color patterns and male nudging of females prior to release of gametes in giant sea bass (*Stereolepis gigas*: Polyprionidae) and white seabass (*Atractoscion nobilis*: Sciaenidae), and suggested that auditory croaking may also be important for the latter. In nonharemic pair-spawners with internal or external fertilization, courtship may also be used in partner choice. The best known examples among internal fertilizers are various poeciliid species in which males circle and perform lateral displays to females, many displaying sexually dimorphic coloration or appendages (e.g., guppies: Kodric-Brown, 1985; swordtails: Basolo, 1990b). Observations of courtship have been described for at least three group-living and internally fertilizing species of the northeastern Pacific: the shiner perch, *Cymatogaster aggregata* and kelp perch, *Brachyistius frenatus* (Wiebe, 1968; Shaw and Allen, 1977; DeMartini, 1988a), and the blue rockfish *Sebastes mystinus* (Helvey, 1982). In outdoor aquaria, male shiner perch established courting sites of about 2 m diameter and courted females as they passed. Males courted females regardless of female reproductive state. Moreover, they courted males that were not exhibiting the male courtship coloration and chased those that were. Courting males often darken, and follow females, quiver and perform lateral displays, often in a rapid pattern in front or alongside of the female. Whether males also release pheromones during this behavior is unknown. Gravid females have blue, black, and gold bars, compared with the more silvery coloration of other females and perform courtship displays similar to those of males. Male darkening during apparent courtship and intermale visual displays has also been observed in three other silvery embiotocids: rubberlip seaperch (*Rhacochilus toxotes*), white seaperch (*Phanerodon furcatus*), and pile perch (*Rhacochilus vacca*) (E. DeMartini, unpubl. obs.). In the blue rockfish, males perform stereotyped lateral displays and caudal fin fanning that includes presentation of the male's highly visible genital papilla to the female (Helvey, 1982).

As expected, the least amount of data on any details of courtship or spawning behavior are available for pelagic species that do not spawn close to shore, such as all or most scombrids, some clupeids, and engraulids. To our knowledge, the only data on the behavior patterns involved in courtship and spawning in pelagic fishes found off California's coast come from captive studies of Pacific bonito (*Sarda chiliensis*) (Magnuson and Prescott, 1966). Courtship in this species is behaviorally dimorphic—females swim with a wobbling motion caused by tilting the body 5–15 degrees from the vertical and depressing the dorsal fin while being propelled by low amplitude, high frequency tail beats; other characteristic female behaviors include circle swimming near the water surface. Males "follow" females, sometimes assume vertically barred feeding colors, often nose the female's caudal fin to initiate wobbling, and perform lateral displays of intense feeding colors, with all vertical fins erected, to other male followers. Actual spawning (evidenced by release of a visible cloud of milt) occurs only if the male and female physically separate from the school to form a temporary pair; females flee from groups of following males (Magnuson and Prescott, 1966).

The spawning habits of coastal pelagic species that group-spawn are better documented, although it is difficult to observe individual behavior. Spawning has been observed in Pacific herring (*Clupea pallasii*), California grunion (*Leuresthes tenuis*), surf smelt (*Hypomesus pretiosus*), and Pacific sandlance (*Ammodytes hexapterus*). During the late fall-winter spawning period, herring amass over shallow algal or seagrass beds along shores of northwest North America. Fertilization is external, and adhesive eggs attach to the vegetation. The release of gametes is so synchronized and massive that water visibility can be reduced to centimeters, and a milt cloud, visible over kilometers, can persist for several days. Although the factors that influence and synchronize the movement of herring to the inshore spawning grounds are unclear, once inshore, spawning appears to be synchronized by a sex pheromone (Stacey and Hourston, 1982; Sherwood et al., 1991; Carolsfeld et al., 1997). Herring collected from spawning aggregations and held in tanks rarely spawn. However, adding a small amount of milt or extracts of dissected testes can induce spawning. This is a rare example of a bisexual releasing pheromone in fishes.

Most visitors to the beaches of southern California are familiar with the massive nocturnal runs of pelagic grunion on fine-sand beaches from March to August. The southern California species (*L. tenuis*) is one of only two known species of grunion and is strictly a nocturnal spawner. Large numbers of grunion wash ashore on waves during two monthly bouts lasting about 3 days, beginning approximately 3 or 4 days after full and new moons. Spawning begins just after high tide and continues for 1 or 2 hours thereafter. Females position themselves vertically (tail-first) in the sand and deposit eggs. Males encircle the bodies of females, releasing large volumes of milt (fig. 19-9). Individuals are then washed back into the water by the next wave. Eggs hatch and larvae are dispersed 2 weeks later during the next series of high tides. In contrast, the other species, *L. sardina*, found in the Gulf of California, spawns during day and night between January and May, depending on the time of highest high spring tide (Thomson and Muench, 1976). The spawning act of this species is also much shorter (less than 10 sec). Thomson and Muench (1976) speculated that this could be attributable to the shorter period, lower amplitude waves of the northern Gulf compared with coastal southern California.

Surf smelt spawn on gravel (rather than sand) substrata in intertidal zones along shores of the Pacific Northwest. Sandlance spawn on fine sand to mixed sand-gravel substrates.

FIGURE 19-9 Spawning California grunion (*Leuresthes tenuis*) on a beach in southern California. Females position themselves vertically (tail-first) in the sand and deposit eggs. Males encircle the bodies of females, releasing large volumes of milt. Photo by M.H. Horn.

Unlike grunion, surf smelt and sandlance eggs are scattered over gravel as the female swims, rather than buried in the substratum (Thompson et al., 1936; Penttila, 1997). Spawning male surf smelt are smaller than females; males are gold compared to the silver-white females. Also unlike grunion, surf smelt runs occur only during the day, from May to September. Sandlance spawn from November to mid-February in Puget Sound, Washington; their diel spawning periodicity however is unknown (Penttila, 1997). Given the evidence for the use of hormonal pheromones to synchronize spawning in osmerids (Stacey and Sorensen, 2002), their use in surf smelt, at least, seems likely.

Diel Spawning and Hatching Patterns

The time of day during which reef-associated fishes spawn and the time of day at which zygotes or larvae enter the plankton have received considerable attention in tropical reef fishes, and sufficient data are available in tropical species to search for or detect generalities and to test predictions of hypotheses to explain the observed patterns (Johannes, 1978; Barlow, 1981; Thresher, 1984; Robertson, 1991; Sancho et al., 2000; Petersen and Warner, 2002). For fishes that release gametes directly into the water column, the time of spawning corresponds precisely with the time zygotes enter the plankton, and the time of day during which fish spawn should reflect the (potentially opposing) effects of time of day on predation risk to and dispersal of propagules as well as adult predation risk, conflicting behavioral demands (e.g., feeding, visiting cleaning stations), and interference with other species. For those species that deposit eggs on the substratum, the time of day of spawning and emergence of larvae into the plankton may not be linked, although the time of laying may affect the diel time of hatching. Thus, the time of spawning may be more likely to be affected solely or primarily by adult biology, and hatching time should be affected by predation risk and possibly factors that affect dispersal in benthic spawners.

Existing data for tropical reef fishes suggest that water-column spawners might differ from benthic spawners in diel time of spawning. Among tropical reef species that release gametes into the water column, spawning times are variable among and even within species and the factors responsible for these differences are unclear. Trends in diel peaks in spawning and egg hatching are much more discernible, however, for tropical reef fishes that deposit eggs on the substratum. Spawning most often occurs during early morning in substrate spawners. Some variation exists that appears to be linked to social structure: dawn spawning peaks appear to be more common among species in which both sexes are territorial than in species in which only nest-guarding males are territorial (Kohda, 1988). It has been suggested that this behavior reflects an adaptive response to changes in the activity patterns of territory intruders, which are lower at dawn than during other daytime periods (Kohda, 1988). Given that most of these data come from studies on damselfishes, which are mostly tropical in distribution, it is noteworthy that garibaldi at Santa Catalina Island, where both sexes are also territorial, spawn throughout the day with no dawn peak (Sikkel, 1995b). Again, sufficient data on diel spawning periods and territorial intruder pressure are lacking for most temperate pomacentrids or temperate representatives for other predominantly tropical groups (e.g., blennioids) to determine whether the departure exhibited by garibaldi is representative of temperate conditions.

Among truly temperate families, or families with many temperate representatives, the hexagrammids, cottids, and clinids appear to exhibit sufficient variation in social structure and other aspects of reproductive ecology to warrant further investigation on determinants of diel spawning cycles in benthic spawners. For example, in the painted greenling (in which both sexes defend territories) back-calculations using egg developmental stages suggest early morning spawning activity (DeMartini, 1985). Opportunistic observations of the confamilial kelp greenling suggest that at least some spawning might occur during mid-day in this species (DeMartini, 1986).

Hatching of substratum-attached eggs occurs exclusively at night among tropical reef species that have been examined (Thresher, 1984; Robertson et al., 1990; McAlary and McFarland, 1993) and is thought to be an adaptive response to predation on emerging larvae. A patient observer can wait near a nest with advanced-stage embryos at dusk and, with the aid of a red light, observe larvae emerging from eggs and swimming toward the surface as darkness falls. Exposure to light during the hatching phase will inhibit hatching (McAlary and McFarland, 1993). To our knowledge, among benthic-spawning representatives found off California and adjacent waters, data are available only for one tropical derivative (garibaldi), which also has nocturnal hatching (Alcalay and Sikkel, 1994). Diel time of hatching in general might be less predictable, hence less subject to related adaptations in diel time of spawning, in temperate species whose spawn masses contain large embryos that develop slowly (often requiring a month or longer to hatch) at cold water temperatures.

Behavioral and Evolutionary Ecology of Reproduction

The reproductive ecology of California marine fishes is certainly most unique and interesting because of its taxonomic diversity and biogeographic variability, attributes which make many of these fishes ideal candidates for comparative studies of mating systems, gender allocation, sexual selection, and parental care. In this section, each of these topics will be considered in turn. California species representatives of several tropical lineages (the serranid subfamily Serraninae, the families Labridae and Gobiidae) exhibit uniquely diverse gender allocation patterns and mating systems. Representatives of the boreal-cold temperate Scorpaeniformes (the family Cottidae in particular), including but not limited to Californian species, are obvious candidates for both phylogenetic and biogeographic studies of parental care.

Mating Systems and Gender Allocation

A fundamental aspect of reproductive ecology is the suite of behaviors, collectively described as mating systems, which describe the reproductive interrelations of individuals in population units (Berglund, 1997). Mating systems in all organisms can be categorized based on the manner in which adults associate to reproduce. Basically there are two qualitatively different modes of mating association: polygamy (in which multiple partners of one or both sexes associate for reproduction) and monogamy (associations limited to singletons of each sex). The former span a range of degrees of extra-pair associations from polygamy to promiscuity (Berglund, 1997).

PROMISCUITY

Truly promiscuous spawning, in which two or more (often many more than two) individuals briefly associate to exchange gametes, is the most prevalent type of mating system in marine and freshwater fishes (Thresher, 1984; Berglund, 1997). Promiscuity is the most prevalent mating type in schooling and migratory (e.g., coastal and open-ocean pelagic) species such as clupeids (sardines, herrings), scombrids (mackerels, tunas), and other open-water fishes. Representative California marine examples among pelagic-spawners span a diverse array of families, from tiny schooling forage fishes like anchovies to huge apex predators such as swordfish. Promiscuous spawners also include site-attached reef-dwellers like painted greenling (DeMartini, 1987) and garibaldi (Sikkel, 1988, 1989) in which individuals of each sex court and spawn sequentially with multiple members of the opposite sex and the male remains to tend broods of benthic spawn. Individual females in paternal egg-tending species that exhibit the latter type of promiscuity include those in which entire clutches (discrete egg productions of females) are completely allocated to one male (painted greenling: DeMartini, 1987) as well as those like garibaldi in which clutches are only partially spawned per spawning bout and the eggs within clutches are distributed among multiple males (Sikkel, 1988). Promiscuous spawning entails more than the absence of any predictable association between the reproductive act and the use of spatial resources such as mating (or feeding) areas. Rather, the fundamental characteristic of promiscuity is successive spawning by both sexes with multiple partners with minimal or no pair-bonding. Brief pair-spawns in which one male and one female exchange gametes usually involve the association of multiple partners in rapid succession and hence constitute promiscuity rather than serial monogamy.

POLYGAMY

Reproductive associations among one male and multiple females (polygyny) and among one female and multiple males (polyandry) conceptually bridge the extremes of promiscuity and monogamy. All polygamous systems entail at least a short-term pair-bond between partners. Included are mate defense systems in which one large, typically male, individual is able to socially dominate a harem of smaller, usually female, individuals. In another type of haremic (resource defense) system, the dominant individual of one sex (again, usually male) has the capability of controlling smaller subordinate (usually female) individuals' access to environmental resources. Fishes like many tropical labrids (wrasses) in which the sizes of individual and collective feeding territories are both a response to and predetermined by body size (Robertson and Hoffman, 1977; Hoffman, 1983, 1985) are representative. Two likely California marine fish examples are California sheephead (Warner, 1975a; Cowen, 1990) and rock wrasse (Diener, 1976; E. DeMartini, unpubl. obs.). A common feature of all polygamous mating systems is that they evolve and are maintained only if the fitness benefits to individuals at a minimum meet some system-specific environmental potential for polygamy, above which polygamous individuals enjoy disproportionate fitness benefits (Emlen and Oring, 1977).

Haremic resource defense systems by definition usually involve some type(s) of reproductive territoriality, which, as already stated, has been well documented for very few California marine fishes. Territoriality in California marine and other fishes is of course not limited to reproduction only. Again, few documented cases exist for California marine fishes. A conspicuous exception is the black perch *Embiotoca jacksoni*, for which an important secondary function of territoriality (feeding) has been experimentally demonstrated by Hixon (1981). Grant (1997) has recently reviewed the general topic of territorial behavior in fishes. Further discussion of nonreproductive territoriality and related agonistic behaviors is beyond the scope of this chapter (see chapter 17 for more information).

MONOGAMY

Monogamy requires more than a short-term, exclusive physical association between two individuals of the opposite sex. Many monogamous fishes are dioecious (Barlow, 1984), but monogamous relationships also occur in which two hermaphroditic individuals spawn with one another exclusively (Pressley, 1981) or nearly so at low population densities (Petersen, 1990b). Among the best-known examples of monogamous hermaphrodites, for which there are no described California examples, are the egg-trading hamlets, a group of small-bodied, site-attached Caribbean serranines (Fischer, 1980). Unstudied California examples of possibly monogamous hermaphrodites are *Diplectrum* spp, small-bodied serranines of southern Baja southward (Bortone, 1974, 1977). At its most extreme, monogamous mating systems extend beyond courtship and spawning to include mutual defense of shared spatial resources such as foraging and sheltering territories, sometimes involving lifetime pair bonds in long-lived species.

There are thought to be three major selective agents favoring monogamy in fishes: the requirement of more than one parent to provide some type of post-zygotic care; paired defense of some spatially delimited resource; and restricted access to mates in sparsely distributed (e.g., small-bodied and site-attached) fishes (Berglund, 1997). The occurrence of simultaneous hermaphroditism within monogamously mated pairs has been described in many species of small-bodied, site-attached tropical serranines besides the hamlets; these likely represent cases of efficient gender allocation and monogamy within sparsely distributed, low-density populations (Pressley, 1981; Fischer and Petersen, 1987).

Known examples of monogamous California marine fishes are few and include a single species of extremely site-attached goby (the blind goby, *Typhlogobius californiensis*: MacGinitie, 1939). The blind goby seems to exemplify small-bodied, site-attached, and relatively immobile species for which restricted access to mates has favored the evolution of monogamy (Barlow, 1984). Monogamous pairs of blind gobies exhibit biparental care of demersal eggs within their burrow, and the species is apparently dioecious (MacGinitie, 1939). Predation risk is a related and complementary selective agent favoring monogamy in small-bodied, site-attached species (e.g., many coral-inhabiting gobies: Munday et al., 1998). Aquarium observations suggest that monogamy may also be the norm in the large-bodied (to >2 m) wolf-eel (Marliave, 1987), but more long-term field observations are needed to substantiate this.

In the freshwater tropics, many species of cichlids form monogamous bonds that are required for both parents to feed and protect free-swimming young from predators (Perrone and Zaret, 1979). There are no described or likely cases of monogamy required for biparental provisioning of young among California marine fishes. There also are no known or likely cases of paired defense of spatial resources, such as the feeding territories of corallivorous chaetodontids on coral reefs.

The relation between synchronous hermaphroditism and monogamy provides but one example of the linkage between mating systems and gender allocation. The size-advantage model, whereby the largest, most dominant individuals of the limiting (usually male) sex are able to sequester the most or best of environmental resources such as spawning sites (Berglund, 1997), amply describes the evolution of promiscuity and/or harem polygyny and protogynous sex change in many lineages of tropical coral reef fishes. The size-advantage model can be briefly summarized as follows: under conditions of intense competition for resources, lifetime individual reproductive success can be maximized if individuals spawn as females when small (and incapable of securing access to high-quality resources and female mates, were they to first mature as males) and as males when large and capable of securing access to resources and females (Warner, 1975b, 1988a,b). Protogyny has thus far been described for diverse lineages representing at least 17 families of reef and other inshore tropical fishes worldwide (table 19-2), a proportion greatly exceeding that in the resident California marine fauna (table 19-3). Protandry has been described in fewer families, also primarily tropical in origin. Protandry may be driven by "fecundity selection" in which the largest-bodied females are inordinately fecund, and represents another expression of the size-advantage model (Warner, 1975b, 1984).

Three primarily tropical families (Serranidae, Labridae, and Gobiidae) are well-represented by species in California for which protogynous sex change and promiscuity/polygyny is either known or likely. It is intriguing that, in California waters, all three of these families also include species that comprise at least some gonochoric individuals (all mature individuals derived directly and independently from immature fish). For example, among California serranines, barred sand bass (*Paralabrax nebulifer*: Oda et al., 1993) and spotted sand bass (Hastings, 1989; Hovey and Allen, 2000) have populations composed of protogynous as well as gonochoric males. Smith and Young (1966) described the kelp bass *P. clathratus* as a secondary gonochore evolved from a hermaphroditic ancestor, although incomplete histological evidence presented therein and limited additional evidence (Oda et al., 1993) suggest some degree of bisexuality or sex change in some individuals. Likewise among the California Labridae, California sheephead (Warner, 1975a; Cowen, 1990) and rock wrasse (Diener, 1976) are protogynous, while the senorita, *Oxyjulis californica*, is a gonochore (Diener, 1976). Rock wrasse, unlike the monandric sheephead, are diandric (populations comprise adult males derived from two sources—secondary males derived from sex-changed adult females and primary males derived directly from undifferentiated immature fish: Diener, 1976).

Among the gobies of California, protogyny has been documented in the blackeye goby (Cole, 1983; Cole and Shapiro, 1990) and protogyny, simultaneous hermaphroditism, and bidirectional sex change have been described for *Lythrypnus* spp. (St. Mary, 1993, 2000). Gonochorism is the most probable type of sexuality, however, in several other California gobiid genera (*Ilypnus*, *Quietula*, and *Clevelandia*: Brothers, 1975). Whether gonochorism in these and other gobies is primary, or secondarily derived from protogynous ancestral lineage, is generally unknown but now amenable to scrutiny using a histological-morphological metric (precursive accessory gonadal structures, pAGS), whose absence in the ovarian wall of most if not all female gobiids indicates secondary gonochorism (Cole et al., 1994). There are at least another dozen species of California Gobiidae for which gender allocation is totally unknown.

In all three of these groups of fishes, there appears to be a temperate-tropical pattern to the distribution of gender allocation types. For example, although some temperate-zone serranines are protogynous hermaphrodites (e.g., *Centropristes striatus* in the western Atlantic: Lavenda, 1949) or comprise populations of mixed gonochores and protogynous hermaphrodites (some California populations of spotted sand bass: Hovey and Allen, 2000), all of the two to four known secondarily gonochoric species of serranines occur in temperate waters.

Kelp bass may be the only completely gonochoric serranine of California. All California serranines might be derived from hermaphroditic tropical ancestors (Smith and Young, 1966), but recent phylogenetic evidence casts doubt on this hypothesis (Pondella et al. 2003). The only other definite, secondarily gonochoric serranine is the South American species, *Paralabrax humeralis* (Borquez et al., 1988). Sex ratios suggest that the golden spotted rock bass *Paralabrax auroguttatus* is a gonochore in the northern Gulf of California (Pondella et al., 2001). The barred sand bass may be a functional gonochore derived from a protogynous ancestor (Hovey et al., 2002). Allied temperate-zone gonochores are the striped bass (*Morone saxatilis*) of the east coast of North America (purposely introduced to the San Francisco Bay estuary from the Atlantic USA in the late 1800's: Scofield, 1931), the European sea bass *Dicentrarchus labrax* of the eastern Atlantic and Mediterranean (Pawson and Pickett, 1996), and the Atlantic wreckfish *Polyprion americanus* (Roberts, 1989). These allied species are temperate sea basses of the families Moronidae and Polyprionidae. A California example of the latter family is the fishery-protected giant sea bass (Hovey, 2001), whose gender allocation type is unknown. All serranid groupers of the subfamily Epinephelinae thus far studied are monandric protogynous hermaphrodites except for the gonochoric Nassau grouper *Epinephelus striatus* (Sadovy and Colin, 1995) and the diandric *E. andersoni* (Fennessy and Sadovy, 2002), *Cephalopholis boenak*, and perhaps a few others (Chan and Sadovy, 2002). Likewise, all basslets of the subfamily Anthiinae are protogynous, including the minority of species that inhabit temperate waters (Jones, 1980; Webb and

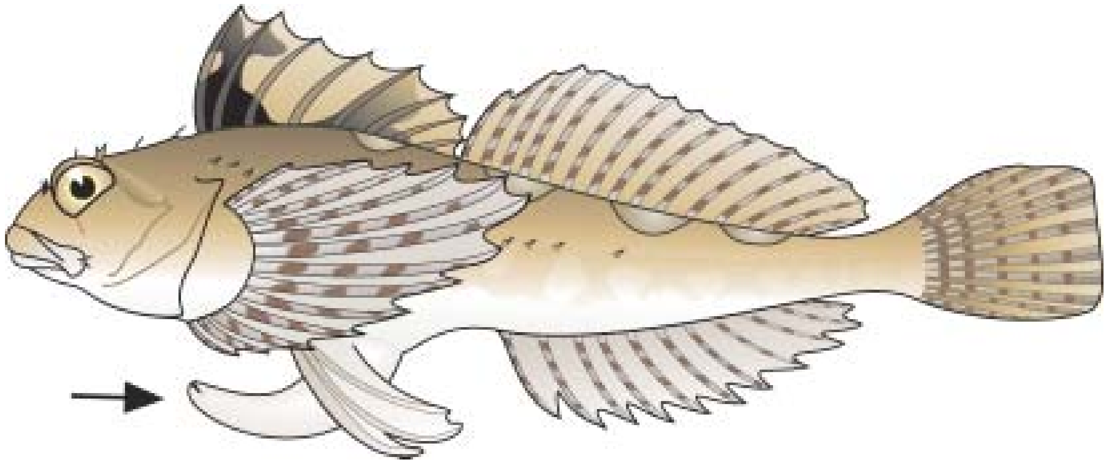

FIGURE 19-10 Adult male of the cottid *Clinocottus acuticeps* showing highly developed intromittent organ in this copulating species (after Bolin, 1944 with permission from Stanford University Press).

Kingsford, 1990). Described gonochoric species within the primarily tropical Labridae comprise only the senorita in California; *Notolabrus fuscus* of temperate New Zealand waters (Denny and Schiel, 2002); and several other, also temperate, species of the genera *Centrolabrus*, *Ctenolabrus*, and *Symphodus* (*Crenilabrus*) in the northeastern Atlantic (Dipper and Pullin, 1979). The latter genera include species with reproductively territorial, dimorphic males; and some species of *Symphodus* care for nests of demersal eggs. It is thought that the cost of paternal care constrains the evolution of sex change in these species (Warner and Lejeune, 1985). The tautog *Tautoga onitis* of the west Atlantic is probably a gonochoristic species with some vestiges of protogyny (White et al., 2003). Gender allocation is unknown in one slightly dichromatic and reproductively territorial, pelagic group-spawning (Wicklund, 1970) labrid of the temperate-boreal west Atlantic, the cunner *Tautogolabrus adspersus* (Pottle and Green, 1979).

We could find no records at all of gonochorism in tropical labrids even though a sister group of tropical labroids (parrotfishes of the family Scaridae) include species of known gonochores as well as monandric and diandric protygynous hermaphrodites (Robertson and Warner, 1978; Robertson et al., 1982). Most gonochoric species of the primarily tropical Gobiidae occur in temperate waters: these include the temperate genera *Gobius* and *Pomatoschistus* and both temperate and tropical species of the genus *Bathygobius* (Cole, 1988, 1990). The only other well-documented gonochores among tropical gobies are *Gobiosoma illecebrosum* and *G. saucrum* (Robertson and Justines, 1982). Most known hermaphroditic species of tropical gobies inhabit coral reefs. All three species of California gobies known to be hermaphroditic (bluebanded, zebra, and blackeye gobies) are rock reef associates; most other species of California gobies inhabit (burrows in) soft substrates.

The available evidence thus strongly suggests that the development of gonochorism in some temperate species of serranine serranids, gobiids, and labrids is related to some aspect(s) of temperate zone environments. Several, possibly interacting factors are discussed in the fourth section.

Sexual Selection and Mate Choice

Sexual selection, the process responsible for the evolution of secondary sexual or epigamic traits (Dugatkin and FitzGerald, 1997), includes two components: intrasexual selection (typically male-male competition) and intersexual selection (mate choice, usually by females). The most conspicuous, hence well-known, adaptations are the secondary sexual characteristics and sexual ornamentation used in behavioral displays between and within the sexes. Unstudied but likely California examples of the latter include the sexually dimorphic, supraorbital crests (fatty forehead tissues) of the crested prickleback *Anoplarchus purpurescens* (Coleman, 1992) and similar, sexually dimorphic head features of the wolf-eel (Marliave, 1987). Possibly analogous head morphologies occur in several other stichaeids (the monkeyface prickleback *Cebidichthys violaceus*, *Xiphister atropurpureus*, and *X. mucosus*: Hart, 1973). Whether the apparent sexual dimorphisms in some of these zoarcoids vary with reproductive seasonality—or even whether they in fact are sexual ornaments—is unknown. Moderate-to-great dimorphisms in body size are especially common and most striking in spawn-tending hexagrammids of the eastern and western Pacific.

Sexual dimorphisms are minor or only temporary, however, in most other lineages of California fishes. Sexual dimorphisms are largely lacking in most groups in which one might expect them, such as the spawn-tending cottids. Most of the male-female differences in cottid morphology and coloration are temporary and related to seasonal reproduction. For example, male red Irish lords (Peden, 1978; DeMartini and Patten, 1979) and scalyhead sculpin *Artedius harringtoni* (Hart, 1973; Ragland and Fischer, 1987) develop pectoral fin spination and hypertrophied head cirri during their respective breeding seasons. Perhaps the most striking morphological difference between the sexes in cottids is the prominent penis of males in some species, a primary rather than secondary sexual characteristic (fig. 19-10; see Bolin, 1944 for other examples). Live-bearing embiotocids also copulate (e.g., see Hubbs, 1917), but male surfperches use a gonopodium of modified anterior anal fin rays (Shaw, 1971) instead of a penis for copulation. In general the extent to which sexual characteristics such as the intromittent organs of males represent intra- *vs*. intersexually selected traits is poorly understood in the cottids, other copulating fishes such as poeciliids, goodeids, and embiotocids, and most other organisms.

Another reproductive trait subject to sexual selection is sperm storage (and related sperm competition) in copulating species with internal insemination. In this regard the North Pacific Cottidae and allied cottoids (Rhamphocottidae, Hemitripteridae, Psychrolutidae) provide an intriguing array of oviparous spawning traits ranging from external fertilization (Hayakawa and Munehara, 1996) to copulation with external fertilization (Munehara et al., 1989, 1991) to external fertilization after copulation by means of a protrusible/retractable female genital duct (Munehara, 1996). Fertilization modes in cottids are overlaid by parental care states that range from paternal to maternal and biparental (DeMartini, 1978b; DeMartini and Patten, 1979; Hayakawa and Munehara, 1996) to no care at all (Marliave, 1981b; Munehara, 1996). Mode of fertilization (internal versus external) has been considered as one reproductive trait that is perhaps both the result of, and further subject to, sexual selection (see Perrone and Zaret, 1979). Although viviparous species by definition copulate and have internal fertilization, some species in at least three genera of oviparous North Pacific marine cottids exhibit copulation with external fertilization (Munehara et al., 1989, 1991; Munehara, 1996). Even though the males of many North Pacific cottids have large intromittent organs (Bolin, 1944), apparently not many cottids with intromittent organs and copulation have internal fertilization. In species like the silverspotted sculpin and elkhorn sculpin (*Alcichthys alcicornis*) of the western North Pacific, sperm attach to, but do not penetrate, the egg micropyle within the ovary post-copulation, and fertilization occurs some time later at the time of egg extrusion. Apparently an increase in chorionic permeability resulting from a change in calcium ion concentration between the ovarian environment and seawater induces penetration of eggs by sperm (Munehara et al., 1989, 1991) as the eggs are extruded. The demersal spawns produced by these species have been described as resulting from external fertilization and internal gametic association (Munehara et al., 1989, 1991). Apparently this is also true for agonids, scorpaeniforms closely related to the cottids (Yabe, 1985); insemination in at least one agonid species occurs by eversion followed by retraction of the female genital duct (Munehara, 1997).

Wonders of physiological and morphological mechanisms aside, the more pertinent questions are what ecological and evolutionary factors have selected for the decoupling of copulation and fertilization and how might this be related to sperm storage, sperm competition, and parental care in this group of fishes. Sperm storage and competition in promiscuous and polygynous species are unavoidably linked to the issue of paternity, particularly in species with paternal care (Perrone and Zaret, 1979). This is true even if the evolution of paternal care is not necessarily precluded by copulation and internal (or delayed) fertilization (Dawkins and Carlisle, 1976). Several case studies have documented paternal care in copulating cottids (Ragland and Fischer, 1987; Munehara et al., 1990, 1994). Data on the distribution of fertilization modes among species of cottids with and without intromittent organs and copulation are lacking. As far as is known, copulating cottids are either promiscuous or polygynous and thus storage of sperm within the female invariably must result in some degree of sperm competition among males (see Koya et al., 2002).

Given the many parental care patterns and the diverse morphologies of spermatozoa (Hann, 1930) in North Pacific cottids, it is almost certain that sperm competition varies greatly among species of sculpins despite the present scant evidence. Unfortunately, empirical proof of sperm competition is lacking for almost all cottid species. Hayakawa et al.'s (2002a, b) recent documentation of a fertilization-shielding sperm morph in *Hemilepidotus gilberti*, a noncopulatory parental-guarder with sneak-spawning males, provides strong circumstantial evidence. Petersen et al. (2004) provided another, more recent example in the roseylip sculpin, *Ascelichthys rhodorus*. Evidence for sperm competition can often be deduced from large testes-to-soma weight ratios (Stockley et al., 1997; e.g., the embiotocid *Micrometrus minimus:* Warner and Harlan, 1982). Data on relative testes weights, however, are nearly nonexistent for cottids. It is likely that copulation has evolved in numerous genera of cottids and cottoids primarily as a ploy to counter sperm competition among males (C. Petersen, pers. comm.) and might not have evolved at all in this group if not for sperm competition (Munehara, 1999).

Sperm competition is a major cost of male reproduction and the storage and mixing of multiple males' sperm within females exacerbates costs to and competition among males (Petersen and Warner, 1998; Petersen et al., 2001). The females of some cottid species store sperm for some time within their reproductive system after copulation. Species like the silverspotted sculpin (Munehara et al., 1991) and Japanese sea raven *Hemitripterus villosus* (Munehara, 1996) copulate some time prior to when eggs are (fertilized as they are) laid, embryos develop slowly through the wintertime period of low productivity, and large feeding larvae hatch into the early plankton bloom when the size spectrum of planktonic prey is suitably large. One possible reason for the delay between copulation and fertilization in these species might be a disconnect between the time for joining of the sexes and the initiation of embryonic development. The initiation of development is likely determined by optimal time for hatching (entry of larvae into the planktonic production cycle), which in turn is a function of the size of individual eggs (larvae-at-hatch), mean water temperature, and rate of embryonic development (Bagenal, 1971; Pauly and Pullin, 1988). Perhaps the delay in hatching of large feeding larvae until early in the next planktonic production cycle has selected for the temporal decoupling of fertilization and copulation in some sculpins.

Not all copulating cottids delay fertilization or store sperm appreciably, however. Male elkhorn sculpin and perhaps scalyhead sculpin appear to tend unrelated spawn (fertilized by a previous copulation with another male) in return for the opportunity to copulate with the female whose spawn they tend (Munehara et al., 1990; Ragland and Fischer, 1987). In cottids lacking appreciable sperm storage, copulation likely has evolved primarily or solely as a response to sperm competition among males.

Parental Care Patterns and Implications

Obviously the most extreme expression of parental care is matrotrophic viviparity. One fascinating group of live-bearing fishes, unique to the North Pacific except for a few species in South American and North Atlantic waters (Moser et al., 2000), are the sebastine scorpaenids of the genus *Sebastes*. In the past simply considered ovoviviparous, the genus *Sebastes* is now recognized as a complex of reproductively as well as taxonomically diverse fishes spanning a range of combinations of offspring provisioning via ovarian egg yolk and maternal nourishment in utero (Wourms, 1991; Hopkins et al., 1995). Some species might be considered nearly ovoviviparous because nearly all embryonic nutrition derives from the yolk sequestered in ovarian eggs (*S. flavidus*: 3% non-yolk; Hopkins et al., 1995). At the other extreme, at least one species (*S. schlegeli*) is extremely matrotrophic in that 92% of embryonic nutrition derives from the extra-oocyte fetal-maternal exchange

TABLE 19-4

Eastern North Pacific Marine Sculpins Known to Exhibit Post-Zygotic Parental Care or Aparental

Species	*Parental Care*	*Reference*
Artedius fenestralis	male	DeMartini and Patten 1979; Peterson et al. 2004
Artedius harringtoni	male	DeMartini and Patten 1979; Ragland and Fischer 1987
Artedius lateralis	male	Petersen et al. 2005
Ascelichthys rhodorus	grouped males	DeMartini and Patten 1979; Peterson et al. 2004
Asemichthys taylori	extraspecific	Kent et al. 1997; D Kent pers.com
Blepsias cirrhosus	none	Munehara 1991
Clinocottus acuticeps	none	Marliave 1981b
Clinocottus analis	none	DeMartini and Patten 1979
Clinocottus globiceps	none	E DeMartini unpubl obs
Clinocottus recalvus	none	DeMartini and Patten 1979
Enophrys bison	male	DeMartini 1978b
Gilbertidia sigalutes	male	J Marliave (pers com) in Matarese et al. 1989
Hemilepidotus hemilepidotus	female/biparental	DeMartini and Patten 1979
Jordania zonope	male	Lamb and Edgell 1986; C. Petersen pers. com.
Leptocottus armatus	male (?)	DeMartini and Patten 1979
Myoxocephalus polyacanthocephalus	male	D Kent, pers. comm.
Nautichthys oculofasciatus	none	DeMartini and Patten 1979
Oligocottus maculosus	none	DeMartini and Patten 1979
Oligocottus snyderi	none	E DeMartini, unpubl. obs.
Orthonopias triacis	none	Bolin 1941; E DeMartini, unpubl. obs.
Rhamphocottus richardsoni	male	Munehara et al. 1999
Scorpaenichthys marmoratus	male	Lauth 1989
Synchirus gilli	none	Marliave 1975; Marliave et al. 1985

NOTE: List includes Cottidae, Hemitripteridae, Psychrolutidae, and Rhamphocottidae.

of nutrients (Boehlert et al., 1986, 1991; Hopkins et al., 1995). Several of the relatively few, additional species thus far studied represent cases of intermediate maternal provisioning (*S. melanops*: 69%, Boehlert and Yoklavich, 1984; *S. caurinus*: 12%, Dygert and Gunderson, 1991). Unlike the embiotocids, some *Sebastes* spp. have evolved superfoetation; individuals of a dozen species produce as many as three overlapping broods per spawning season (Love et al., 1990). Spawning seasons of most eastern Pacific *Sebastes* are protracted even in species without superfoetation. Copulation-fertilization typically occurs at or near the end of a period of relatively high adult food abundance in the fall, when large female energy stores are available to yolk eggs. Following several months gestation, parturition of young is timed to broadly overlap with a peak in planktonic productivity sometime in the spring (Larson, 1991). It is likely that the partially lecithotrophic viviparity of *Sebastes* spp. is an adaptation whereby females are able to incrementally adjust the relative contributions of ovum yolk and subsequent maternal stores to embryo nutrition, depending on unpredictable fluctuations in productivity (MacFarlane et al., 1993; MacFarlane and Bowers, 1995).

Parental care patterns within the order Scorpaeniformes, the family Cottidae in particular, represents an intriguing diversification that might have both phylogenetic and biogeographic elements. In the Cottidae, the locally most diverse group with prevalent parental care that has been fairly well studied to date, both phylogenetic and biogeographic influences are evident. Some genera like *Oligocottus* and *Clinocottus* appear to be aparental, whereas other genera such as *Artedius* and *Hemilepidotus* exhibit care (table 19-4). It is noteworthy that there also appears to be a geographic component to care patterns within the eastern Pacific Cottidae. The relative number of parental caregivers tends to decrease among species with southern affinities (i.e., those whose ranges extend south of Point Conception into the Southern California Bight) although the relationship is not significant (table 19-5A). The sizes of eggs (larvae at hatching) also tend to be larger for eastern Pacific cottids with more northerly distributions ($x^2 = 5.75$; df = 1; $0.02 > P > 0.01$, ns because the 26 species in 18 genera were not independent; table 19-5B). We speculate that there has been stronger selection for post-zygotic care of the larger eggs (larger larvae) necessary to overcome the vicissitudes of larval advection in the more intensely upwelled regions north of Point Conception. Larger embryos whose development is further protracted at colder water temperatures remain at risk longer to reef-based predators and are likely to benefit more from parental care. We caution however that the extent to which phylogeny and biogeography might be confounded within the Pacific marine cottids is unknown. Data are insufficient for more refined analyses of patterns within cottid genera; data on egg production (fecundity and spawning frequency), largely lacking for northeast Pacific cottids, might help clarify patterns of investment at the species level. It is beyond the scope of this review to attempt to map parental care patterns on phylogenies within the Cottidae. C.W. Petersen of the College of the Atlantic, Bar Harbor, Maine, is presently conducting studies of mating and parental care systems in northeastern Pacific cottids.

Filial Cannibalism as a Mating Tactic

Filial cannibalism (the consumption by parents of related offspring) appears to be an important sexually selected trait in

TABLE 19-5

Parental Care and Egg Size of Eastern North Pacific Sculpins

	Above Point Conception	Below Point Conception
(A) Parental care		
with care	83.3 (10)	45.5 (5)
without care	16.7 (2)	54.5 (6)
(B) Median egg size	Above Point Conception	Below Point Conception
egg size above median	71.4 (10)	16.7 (2)
egg size below median	28.6 (4)	83.3 (10)

NOTE: (A) Percentage of species with known parental care (versus no post-zygotic care) in eastern North Pacific (ENP) sculpins whose southern geographic range limits lie at or above versus below Point Conception, California (34.5° N). (B) Percentage of ENP sculpin species with egg size greater than (versus less than) median egg size (1.5 mm, all species) whose southern limits lie at or above versus below Point Conception. Range data: Miller and Lea (1972), Hart (1973). Egg size data: Budd (1940), Washington et al. (1984), Feeney (1987), Tokranov (1988), Matarese et al. (1989), Munehara and Shimazaki (1991), and C. Petersen (pers. comm.; *Artedius fenestralis*: 1.1–1.2 mm; *A. harringtoni*: 0.9 mm; *Jordania zonope*: 1.8 + mm). Numbers in parentheses indicate number of species.

teleost fishes (Hoelzer, 1995; Lindstrom, 2001), and its existence has been confirmed for several species of freshwater sunfishes and darters by genetic typing using microsatellite markers present in tissues of parental males and consumed eggs (DeWoody et al., 2001). Both filial cannibalism and heterocannibalism (consumption of unrelated conspecifics) are now recognized as widespread phenomena among teleost lineages, especially spawn-tending species (Dominey and Blumer, 1984; Elgar and Crespi, 1992; Smith, 1992; Smith and Reay, 1991; Manica, 2002). Apparent filial cannibalism is widespread among hexagrammmid and cottid scorpaeniforms of the Pacific Northwest (DeMartini, 1976), and its importance is recognized for at least one spawn-tending perciform of California (garibaldi: Sikkel, 1994a, b). Although cannibalism of offspring directly benefits the male tending parent energetically, it is often utilized as a mating tactic that appears to enhance the reproductive success of the filial cannibal indirectly and, as a tactic, is thus subject to sexual selection by affecting and being affected by female mate choice (DeMartini, 1987; Sikkel, 1988, 1989, 1994a, b). We conclude this section with a brief further discussion of how filial cannibalism might importantly relate to the mating and parental care systems of the California Hexagrammidae and Cottidae.

One major reason why paternal male spawn-tenders may cannibalize some of their genetic offspring is because prior-spawned embryos serve, depending on context, either as a female attractant or repellant. There are at least several, non-mutually exclusive (and likely complementary) reasons for this. First, the presence of prior spawns signals to prospective future female mates that the male is a good mate/parent, and this might be important for species in which copying is an evolved basis for female choice (e.g., Sargent, 1997). Second, the presence of other females' spawns acts to dilute predation risk over clutches within the male's brood (akin to the "safety in numbers" effect of schooling). Third, the presence of early-development (visibly uneyed) embryos signals that a male is early in its mating cycle and hence more likely to accept and defend the prospective female's clutch until hatching. Conversely, the presence of late-development (visibly eyed) spawn is a signal that a prospective female's clutch would more likely be eaten as an investment towards increasing the male's future reproductive success. In general, the younger eggs in mixed-age broods are more likely to be partially filial cannibalized and relatively small broods (e.g., single clutches) are more apt to be completely filial cannibalized by paternal males. All of these factors have been documented to varying degrees in painted greenling (DeMartini, 1987) and garibaldi (Sikkel, 1994a,b). However in the latter, the cannibalism of relatively older (but still young) eggs is dependent on their position in the nest and the phase of the brood cycle (Sikkel, 1994a).

Cannibalism by male spawn-tenders also might be a tactic to counter cuckoldry by sneak-spawning, nonterritorial males. Heterocannibalism (Rohwer, 1978) therefore is likely more complex than mere raiding among neighboring spawn-tenders. Although egg cannibalism is widespread in the Hexagrammidae, the occurrence and nature of filial cannibalism has been questioned in some species (Munehara and Miura, 1995). The occurrence and activities of sneak-spawning males have recently been documented in numerous species of western north Pacific hexagrammids (*Hexagrammos otakii*, *H. octogrammus*, *H. agrammus*: Munehara et al., 2000; Munehara and Takenaka, 2000). Both in situ remote video records (Munehara at al., 2000) and genetic evidence of multiple paternity in single-male-tended broods (Munehara and Takenaka, 2000) have been demonstrated. An important counterpoint: genetic evidence also has shown that multiple females contribute clutches to single-male-tended broods in kelp greenling (Crow et al., 1997) and other fishes such as mottled sculpin *Cottus bairdi*, a freshwater cottid (Fiumera et al., 2002). *In situ* observation of spawning has also confirmed multiple-female contributions to male-tended clutches in many other fishes, including garibaldi (Sikkel, 1988).

The occurrence of filial cannibalism selects for additional mating ploys and counterploys. One such ploy might be alloparental care. Alloparental care of non-kin spawn has been described for males of the elkhorn sculpin. In elkhorn sculpin, males usually tend embryos that they have not fathered after they copulate with the female who has spawned them (Munehara et al., 1990, 1994). Male care of unrelated eggs in this case is not cuckoldry (as care of non-kin fertilized by sneak-spawners would be), but more likely reflects females' trading copulation for paternal care (Munehara et al., 1994). That unrelated eggs are used as courtship dummies (Rohwer, 1978) in elkhorn sculpin is further supported by the observation of frequent male desertion of nesting sites near the end of the spawning period when the expectation of future spawnings is low. Using prior spawns to attract additional females is commonplace in promiscuous male spawn-tenders. Elkhorn sculpin are highly promiscuous and males tend the clutches of tens of females over a protracted spawning period (Munehara et al., 1990). Piracy, an extreme form of alloparental care in which the most dominant male individuals usurp the spawning territories and nesting materials of other, territorial but subdominant males, spawn in the latter males' territories, then desert spawn to defense by the cuckolded males, has been described in some peacock wrasse (*Symphodus tinca*) populations in the Mediterranean (van den Berghe, 1988). Alloparental care and cuckoldry, however, should not be assumed prevalent in all species of paternal-tending fishes (e.g., mottled sculpin: Fiumera et al., 2002).

Also documented are several other fascinating behaviors that may be evolved responses by males and females to filial cannibalism or some other tactic related to asymmetric parental investment by the two sexes. One recognized ploy involves egg mimics (egg-like protuberances and color spots on the anal, pelvic, or dorsal fins of male darters of the family Percidae: Knapp and Sargent, 1989; Strange, 2001; Porter et al., 2002), which apparently function to deceive prospective female mates by advertising that males already possess more tended spawn than they in fact do. Possible California examples include the scalyhead sculpin, in which males develop apparent egg mimics on their anal fin during the breeding season (Ragland and Fischer, 1987), and male red Irish lords and other North Pacific hemilepidotine cottids (Peden, 1978) that acquire white spotting on darkened pelvic fins during their breeding seasons. Another counterploy, this time performed by females of a species of filial cannibalistic warm-temperate blenniid (Kraak, 1996), is the partial spawning of 1 to 10 test eggs that may be used to evaluate the prospective male's ability and willingness to tend the female's full complement of several hundred eggs (Kraak and van den Berghe, 1992). Another recently discovered female counterploy is the provision of low-energy (unyolked) dummy eggs in the male mouth-brooding cardinalfish *Apogon lineatus* (Kume et al., 2002). In this species, in which males disproportionately cannibalize smaller-than-average-sized clutches, females perhaps deceive males by producing clutches that on average contain about 18% unyolked eggs; these seemingly large clutches might be less filial cannibalized by males (Kume et al., 2002).

Gender Allocation and Parental Care in Temperate versus Tropical Environments

California marine fishes exhibit a diverse array of mating systems and related sexually selected traits such as dimorphisms and filial cannibalism, but neither the frequency of occurrence nor degree of expression of these traits is unusual compared to fishes elsewhere. Eastern north Pacific fishes are exceptional only in the preponderance of viviparous and parental-caring species. And, although not unique to California, the occurrence of secondary gonochorism in species within three distinct lineages of tropical origin in California showcases a phenomenon common to other temperate regions. So why might viviparity and other, less extreme forms of parental care have evolved so frequently in so many lineages of California marine fishes? And, why might the development of secondary gonochorism be such a uniquely temperate phenomenon?

Perhaps these questions might be more appropriately rephrased as: "Why is parental care not more prevalent on tropical reefs?" and "Why is hermaphroditism and sex change relatively common in tropical, but not temperate, reef fishes?" We believe that the interactions among several environmental factors (habitat persistence, on- versus off-reef egg predation, the environmental potential for polygamy [EPP] of adults) provide at least partial answers to these questions. In the remainder of this section, we discuss each of these factors in terms of their effects on gonadal allocation and parental care.

Hermaphroditism and Secondary Gonochorism

Two major factors promoting the evolution of simultaneous hermaphroditism (and monogamy) are low adult densities and small home ranges (Jones, 1980), the latter often related to small adult body size (DeMartini, 1997). Greater numbers of species of predominantly small and rare fishes occur per unit habitat area in tropical versus temperate seas (Fishelson, 1989). Home ranges of small-bodied species tend to be more constrained because smaller-bodied species must be more site-attached to avoid predation (DeMartini, 1997), and the diversity and relative abundance of predatory fishes is generally greater on tropical versus temperate reefs (Parrish, 1990; Ebeling and Hixon, 1991; Hixon, 1991; Friedlander and DeMartini, 2002). The movements of all fishes, but especially small-bodied species, are more constrained on tropical reefs—all other anti-predator tactics such as schooling being equal. It is thus easy to visualize how monogamously paired, simultaneous hermaphrodites might have evolved on tropical reefs.

The evolution of sequential hermaphroditism, protogyny in particular, also might be favored on tropical reefs wherever the EPP and inter-individual variance in fitness are greater and there is more extreme intra- and inter-sexual competition for mates. In tropical reef fish populations occurring at greater than sparse densities, individuals of the same and the opposite sex typically compete for multiple partners and often exhibit size-based dominance and related extreme variations in individual reproductive success (Warner et al., 1975; Warner, 1984).

Secondary sexual dimorphisms and dichromatisms are especially pronounced in protogynous groups such as the tropical labroids. Body size obviously influences the potential for sequential sex change. Larger-bodied species have greater scope for size-based dominance relationships, and sequentially hermaphroditic fishes tend to attain larger adult size than simultaneously hermaphroditic species (Smith, 1965; Jones, 1980). The most striking examples of these are the serranine and epinepheline serranids: serranines are typically <20 cm long, whereas many of the epinepheline groupers attain lengths of more than a meter (to >2 m in *Epinephelus lanceolatus*; Myers, 1999).

Sexual competition for mates may be less on temperate reefs because the production (and tending) of demersal eggs constrains mate monopolization. Prime spawning sites which function to launch planktonic eggs to avoid reef-based egg predators, avoid predators on spawning adults, and which provide disparately large fitness payoffs (Warner and Schultz, 1992; Warner and Dill, 2000), also may be more economically defensible and monopolizable on tropical reefs. We further suggest that tropical and temperate reef systems generally differ in the spatial and temporal dispersion patterns of reproductive resources that include available members of the potentially limiting (usually female) sex to the limited (male) sex. The evolution of resource defense mating systems is likely facilitated by fundamental territoriality (Emlen and Oring, 1977; Grant 1997) that may be more prevalent among tropical reef fishes. To the extent that reproduction is aseasonal (or at least less seasonal) and more temporally asynchronous among females on tropical reefs, there should be further selection for polygamous matings (Emlen and Oring, 1977). Because of the fitness costs in maintaining simultaneous hermaphroditism under conditions conducive to multiple promiscuous matings as gonochores, selection should favor the development of secondary gonochorism on temperate reefs because the potential fitness payoffs are inadequate for extreme polygamy and sequential sex change to evolve and be maintained.

Hermaphroditism and parental care have variously influenced the development of one another in labrids, gobiids, and serranine serranids. Care patterns reinforce gender allocation patterns in the Labridae; at least some species in one of three temperate northeastern Atlantic genera have evolved paternal care and all of these are gonochoric (Warner and Lejeune, 1985). Parental care patterns complicate gender allocation in both temperate and tropical Gobiidae, however. Californian and other *Lythrypnus* spp. exhibit paternal care despite simultaneous and bidirectional hermaphroditism (St. Mary, 2000). Many tropical gobiid genera such as *Gobiodon*, *Trimma*, *Priolepis*, and *Bryaninops* exhibit paternal care, yet pair monogamously as simultaneous or even bidirectional hermaphrodites (Kuwamura et al., 1994; Nakashima et al., 1995; Sunobe and Nakazono, 1993, 1999; Munday et al., 2002). These cases may represent frequency-dependent dynamic tradeoffs between the competing benefits of hermaphroditic monogamy and paternal care-gonochorism in extremely site-attached habitat-specialists (Munday et al., 1988; Munday, 2002). Parental care of course does not complicate gender allocation in all hermaphroditic fishes—serranines for example spawn pelagic eggs and lack parental care (Thresher, 1984; Fischer and Petersen, 1987).

Interestingly, the only other family of primarily tropical reef fishes that is conspicuously present in California is the Pomacentridae (damselfishes), and both of two species (garibaldi and blacksmith *Chromis punctipinnis*) exhibit paternal care of demersal spawn and are gonochores (Turner and Ebert, 1962; DeMartini et al., 1994). The relation between parental care and gender allocation is more complicated in tropical pomacentrids. All known species of pomacentrids exhibit paternal care and all limit care to demersal spawn except for *Acanthochromis polyacanthus* and two *Altrichthys* species in which both parents additionally tend free-swimming fry after hatching (Thresher, 1985; Leis and McCormick, 2002). But not all tropical pomacentrids are gonochores. Most or all species of the genus *Dascyllus* are protogynous hermaphrodites (Godwin, 1995; Asoh et al., 2001). All anemonefishes of the subfamily Amphiprioninae thus far studied are protandrous hermaphrodites, and most species are monogamous and have paternal or biparental care (Moyer and Nakazono, 1978). Presumably, protogyny in *Dascyllus* spp. is due to extreme male disadvantage at small body sizes (Godwin, 1995) rather than the cost of paternal care and selection against sex change, and protandry in anemonefishes likely reflects fecundity selection. It would seem that the influence of parental care on gender allocation varies among tropical fish lineages. Nonetheless, the growth (and perhaps survivorship) costs involved in sex change should select against hermaphroditism when the competing costs of parental care are as large as generally occur on temperate reefs.

Viviparity and Parental Care

Parental care in tropical reef fishes is likely disfavored in part because of greater selection for the planktonic dispersal of propagules away from benthic habitats whose persistence is less assured. The preponderance of planktonic spawners (versus live-bearers and demersal egg-brooders) on coral reefs must in part reflect the greater probability that suitable habitat patches will disappear in between fish generations due to the occurrence of relatively frequent, major physical disturbances like hurricanes (Barlow, 1981; reviewed in Sale, 1991). Parental care on tropical reefs is also likely constrained by the relatively high risk (compared to temperate reefs) of demersal egg loss to benthic-feeding fishes (Johannes, 1978). The mortality rates of planktonic eggs and larvae clearly are high for both temperate and tropical reef fishes; even so, relative on- *vs.* off-reef egg survivorships must differ between temperate and tropical reefs. It appears that the higher probability of predation on demersal eggs in the tropics has restricted the evolution of demersal spawning to lineages with special anti-predatory adaptations. These comprise fishes that benefit from multiple defenses by nesting in large colonies such as some pomacentrids (in California: Panamic sergeant major *Abudefduf troschelii*: Lott, 1995; blacksmith: Turner and Ebert, 1962) and balistids (Gladstone, 1994; Kawase, 1998), and species that utilize various types of additional protection for eggs spawned on exposed surfaces such as proximity to stinging anemones in *Amphiprion* spp. anemonefishes (Moyer and Nakazono, 1978) or that have toxins in eggs (the pufferfish *Canthigaster valentini*: Gladstone, 1987). Also included are small-bodied (<5–10 cm long), burrow- and tube-dwellers (gobiids and chaenopsids like *Emblemaria hypacanthus*: Hastings, 1992), which possess a physical refuge for their spawn as well as themselves. Many species of small-bodied (<10 cm long) tropical coral reef fishes that are site-attached to shelter both as adults and juveniles as an anti-predator adaptation might provide parental care of eggs after oviposition in part because small body size limits fecundity and low fecundities constrain dispersal (Barlow, 1981). Several species of tropical batrachoidids (e.g., *Amphichthys cryptocentrus*: Hoffman and Robertson, 1983) are unusual in that individual males of these relatively large-bodied (to 25 cm) species tend demersal spawn and fry within excavated burrows in which the male also shelters. Unlike the situation in California and other temperate regions, care of spawn on exposed surfaces of coral reefs by lone individual fish, without some additional means of protection such as that afforded by synchronous nesting (e.g., among neighboring male pomacentrids), is at least extremely rare because of predation risk to eggs and perhaps also egg-tenders. Demographic studies comparing populations of species inhabiting a broad range of predation intensities on temperate and tropical reefs would be needed to test this hypothesis, such as comparative characterizations of the survivorships of both adult spawners and tended demersal egg masses for matched temperate and tropical congeners like damselfishes of the genus *Chromis*.

Upwelling off Pacific North America and Its Effects

Environmental dichotomies between tropical and temperate reefs alone cannot explain the observed differences in parental care patterns between the Pacific coast of North America and other temperate regions. Although temperate waters everywhere vary more seasonally than the tropics, environmental uncertainty in temperate regions is represented in the extreme by upwelling systems such as that off of the coast of California and the Pacific Northwest. We speculate that the dynamic nature of upwelling has influenced the proliferation of viviparity and parental care in eastern North Pacific marine fishes, particularly those off California. Much of the western coast of North America including California lies in an intense upwelling system that is highly productive but also spatially heterogeneous and temporally variable (Brodeur et al., 1996; McGowan et al., 1996; Rebstock, 2003). In this uncertain environment, the natural mortality rates of planktonic eggs and larvae are high, variable, and unpredictable. As part of the price paid for facilitated dispersal by currents, sufficient concentrations of the planktonic prey of fish larvae are patchily distributed, and planktonic fish eggs and larvae are also subject to advection (physical transport) offshore to habitats unsuitable for older benthic stages (Parrish et al., 1981). Upwelling markedly influences both the dispersal and survival of pelagic propagules (e.g., see Ainley et al., 1993). Environmental uncertainty has been proposed to be an important factor that explains the apparently greater preponderance of parental care in freshwater fishes, although the difference may be due to phylogenetic bias (Gebhardt, 1987).

The effects of upwelling are obvious even at relatively small spatial scales in the waters off California. The Southern California Bight represents an oceanographic (Barnett and Jahn, 1987) and biogeographic (Horn and Allen, 1978) ecotone wherein the recruitment of subtropical (and occasionally some tropical) species, transported as eggs and larvae from downcoast breeding populations, is favored whenever upwelling is relaxed during El Niño Southern Oscillation (ENSO) periods (Cowen, 1985). The relatively large young produced by parental-caring and especially live-bearing species tend to more closely resemble the species' later developmental stages, both morphologically and behaviorally, and are more capable of actively maintaining station (Marliave, 1986), thereby reducing mortality from advection. A striking example of an adaptation to disturbance-facilitated dispersal is provided by *Aulorhynchus flavidus*, a paternal-tending tubesnout of California and eastern North America, which disperses eggs and fry in constructed nests anchored to detachable kelp fronds that are rafted to other kelp beds following storm dislodgment (Marliave, 1976).

Future evaluations should compare the patterns of viviparity and parental care among fishes of temperate and tropical lineages in other upwelling systems (e.g., the subtropical eastern South Pacific, west Africa). Potential contrasts should also include temperate regions that lack persistent upwelling, such as much of the Pacific coast of Asia. The latter contrasts should adjust, as necessary, for biogeographic influences within major taxa such as the Embiotocidae, Cottidae, and the scorpaenid genus *Sebastes*, whose distributions bridge the eastern and western North Pacific (see chapter 1).

A General Model of Temperate-Tropical Dichotomies

In general, substantial investment in parental care reinforces selection against sex change, hence selects for gonochorism, at least in large-bodied mobile species that (unlike smaller-bodied, site-attached species for which egg defense within shelters may be less costly) are less strongly tied to shelter for protection. The energetic and survival costs of parental care are now well recognized (Sargent, 1992; Smith and Wootton, 1995), and these costs obviously can constrain the potential for sex change. Care of offspring also lowers the advantage of sex change because mate choice by the limiting sex tends to restrict the extent of mate monopolization by the limited sex (Warner and Lejeune, 1985). Parental care thus is prevalent in temperate systems but is a relatively rare phenomenon among tropical fish lineages because, we suggest, the greater costs of producing and defending large offspring, coupled with the lower payoffs for simultaneous or protogynous hermaphroditism, doubly favors the development and maintenance of gonochorism in temperate reef fishes. We provide a simple graphic model (fig. 19-11) illustrating how tropical-temperate reef differences in EPP and the need for parental care of large propagules in environments with differing ratios of on- versus off-reef offspring mortality might have favored the evolution of both sequential and simultaneous hermaphroditism in coral reef fishes, countered its primary evolution in temperate-zone lineages, and may favor its secondary loss in tropical lineages on temperate reefs.

Summary of Patterns and Promising Topics for Future Research

Summary

Like marine and freshwater fish assemblages elsewhere, the fishes of the Californias exhibit diverse reproductive modes, life histories, and mating and parental care systems. Species exhibiting viviparity and post-spawning parental care are unusually prevalent in the California marine fish fauna, however, and this prevalence is expressed both in terms of the number of species and the number of lineages (families) represented. Altogether, about 150 species (17%) of California marine fishes are viviparous, including 56 species of elasmobranchs (32 selachians in 12 families and 24 species in eight families of rays). The remaining 93 species of viviparous teleosts include all of the 20 marine species of Embiotocidae that occur in the eastern Pacific, nearly 70 species of rockfishes of the genus *Sebastes* (Scorpaenidae), and four genera of viviparous brotulas of the family Bythitidae. Post-zygotic parental care of demersal eggs occurs in at least another 125 oviparous species of batrachoidids, scorpaeniforms (four families), and many gobiid and blennioid perciforms. Most (>90%) California species with parental care exhibit exclusively paternal care, a fraction typical for marine bony fishes (Blumer, 1979, 1982).

Another conspicuous aspect of the reproductive ecology of California marine fishes involves patterns of gender allocation within families of primarily tropical origin. Both gonochoric and hermaphroditic species are conspicuously represented within three marine fish families (the Labridae, Serranidae, and Gobiidae) in California waters. It must be more than coincidence that both gonochoric and hermaphroditic species are present in each of these three families in the temperate North Atlantic as well and that no temperate-zone lineages in either area include both hermaphrodites and secondary gonochores. Clearly, some common features of temperate zone environments influence the expression of hermaphroditism in a manner independent of phylogeny.

We offer a conceptual model suggesting that both parental investment (viviparity and post-zygotic parental care) and biogeographic patterns of gender allocation are related to the unpredictably variable oceanographic environment of the California upwelling system. The rocky inshore fishes of the Californias have evolved in productivity regimes that are both spatially and temporally variable and unpredictable, even though the scope for temporal fluctuations is greater north of Point Conception compared to the Southern California Bight. Point Conception is a long-recognized biogeographic boundary that represents an important productivity threshold as well. Differences in parental care and related gonadal investment per offspring above and below Point Conception are suggestive in at least one family (Cottidae). Tropical reef fish

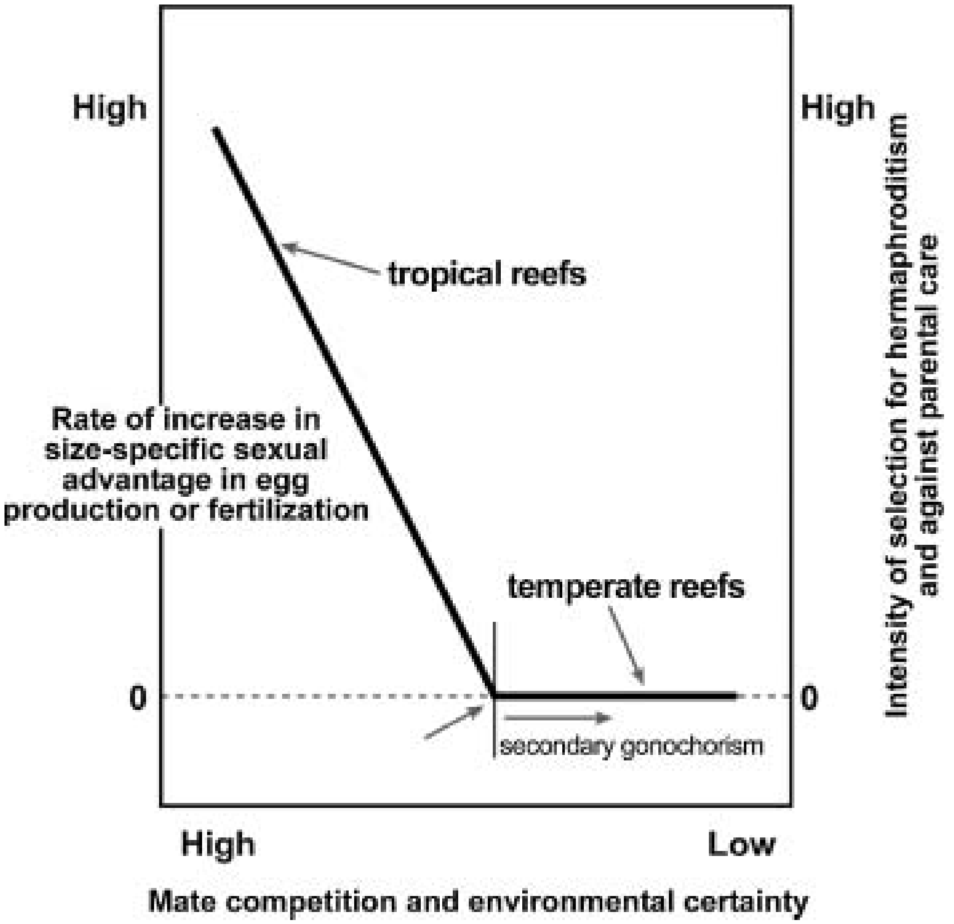

FIGURE 19-11 Conceptual model depicting the relative influences of various environmental factors selecting for sequential sex change and its loss (secondary gonochorism) in tropical and temperate fish lineages.

families are largely restricted to the generally lower productivity regime of the Southern California Bight. We argue that the more variable and less predictable environments north of Point Conception (and extending north of California through the Pacific Northwest) have placed a premium on greater degrees of parental investment (viviparity, care of benthic spawn) in temperate-boreal lineages to augment offspring survival at the expense of adaptations (such as sex change) related to inter- and intra-sexual competition for mates. The secondary loss of flexible gender expression in some species within tropical lineages (serranine serranids and labrids) most likely reflects the discontinuance of sufficient selection for sex change, resulting from lower maximum extents of polygamous mate monopolization. The next challenge will be to respecify this general model as testable hypotheses and conduct the detailed field observations and controlled experiments necessary to test them. This will not be easy. For example, a study of matched gonochoric-protogynous species or populations of *Paralabrax* would at a minimum require comparative estimates of size-specific egg production and the mean and variance of relative mating success, if not the absolute frequency and fertilization success of matings by numerous individuals.

Promising Research Topics

A number of poorly studied families of deep-sea and open-ocean fishes like the stomiiforms, aulopiforms, and lampridiforms, and several virtually unstudied families of benthic shelf fishes such as the agonids, cryptacanthodids and zoarcids, require fundamental surveys of their reproductive natural and life histories. Without information on these groups, our understanding of the diversity and breadth of reproductive adaptations of the California marine fish fauna will remain incomplete.

The environmental and demographic factors influencing maternal investment patterns in live-bearers (embiotocids and *Sebastes* spp.) are another obvious research topic. Some data already exist for surfperches (Warner and Harlan, 1982; DeMartini, 1988a; Schultz et al., 1991; Schultz, 1993; Schultz and Rountos, 2001). Additional studies of the effects of differing relative maternal and paternal investments on sperm storage and sperm competition among embiotocid species are needed. Also necessary are additional characterizations of the levels of maternal investment exhibited among species of the genus *Sebastes*, particularly in terms of the importance of seasonal and interannual variations in upwelling and planktonic productivity on the relative contributions of lecithotrophy and matrotrophy and how these might be affected by species differences in trophic biology. No comparative information of this nature presently exists for sebastine scorpaenids. These and other topics for future research are summarized in table 19-6 and discussed in the paragraphs that follow.

Further studies of the reproductive ecology of several other families of teleosts hold great promise for biogeographic (tropical versus temperate) comparisons. Studies of the relatively few Californian representatives of tropical fish families could provide much useful information for comparison with confa-

TABLE 19-6

Key Topics for Future Research on the Reproductive Ecology of California Marine Fishes

Comparisons of relative maternal investment among species of rockfishes (F. Scorpaenidae) and surfperches (Embiotocidae)

Studies of the relationship between degree of maternal investment and species' trophic biology in rockfishes (*Sebastes*)

Evaluation of latitudinal effects on maternal investment in species with extreme geographic ranges (Embiotocidae: shiner perch, pile perch; Gobiidae: blackeye goby)

Latitudinal comparison of gender allocation patterns among populations spanning the geographic range of blackeye goby

Comparative estimates of survivorship of breeding adults and tended embryos for matched temperate-tropical congeners (e.g., within the pomacentrid genus *Chromis*)

Evaluation of relative sperm competition among species of copulating and non-copulating sculpins (Cottidae) and allied cottoids

Estimation and comparison of testes weights as an index of male reproductive effort in cottoids

Among-species comparisons of cottoid egg production (individual fecundity and spawning frequency)

General description and comparison of gender allocation patterns within the California Gobiidae

Evaluation of the relation between gender allocation and parental care in the Pomacentridae

Comparisons of size-specific egg production and the mean and variance of mating success among gonochoric and protogynous individuals within populations exhibiting mixed gonochoric-protogynous gender allocation (Serranidae: spotted sand bass, barred sand bass, kelp bass)

Analogous comparisons of mating success among species within families exhibiting mixed gender allocation patterns (Serranidae, Labridae, Gobiidae)

General re-examination of distribution of secondary gonochorism among gonochoric species within families exhibiting mixed gender allocation patterns

Comparison of viviparity and parental care patterns for fishes with temperate and tropical lineages, among lineages present in California and other NE Pacific waters, other upwelling systems (like subtropical eastern South America and west Africa), and temperate non-upwelling regions like Japan and temperate eastern Australia

Evaluation of mate choice and intra- versus inter-sexual selection in local examples of likely "sex-reversed" syngnathid pipefishes

Comparisons of diel spawning and demersal embryo hatching times for temperate versus tropical fish lineages of California and other regions such as temperate eastern Australia

milials in tropical regions. Tropical families represented in California and Pacific Baja waters are the Apogonidae (one species), Batrachoididae (two species), Chaetodontidae (two species), Gerreidae (at least 10 species), Gobiidae (20 species), Labridae (five species), Mullidae (two species), Pomacentridae (three species), Scaridae (one species), Serranidae (18 species), and Synodontidae (three species) (Miller and Lea, 1972; De la Cruz Aguero et al., 1997). Only the batrachoidids, gobiids, labrids, pomacentrids, and serranids, however, include species that are sufficiently common and abundant to offer further promise for detailed behavioral study. Analogous evaluations of the effects of temperate environments on reproductive strategies are needed for tropical fish lineages in other regions such as Japan and eastern temperate Australia.

In particular, we stress the great potential for comparative studies of the mating systems and sex allocation patterns among gonochoric and protogynous species populations of the serranine serranids, labrids, and gobiids of California. Further studies of gender allocation patterns are needed, particularly the interplay between gonochoric and protogynous hermaphrodites within species-populations of barred sand bass and kelp bass, similar to that of Hovey and Allen (2000) for spotted sand bass. Inter-populational comparisons also are needed, particularly for species with ranges (like *P. humeralis* of Chile-Peru) that span tropical and warm temperate latitudes, as are interspecific comparisons within the genus *Paralabrax*. A general survey of gender allocation patterns in the California Gobiidae is also needed, including geographic comparisons among species-populations. Currently of great interest is the bewildering diversity of sex allocation patterns (protogyny, simultaneous hermaphroditism, bidirectional sex change) exhibited within and among populations of some gobiids, both in California and on tropical coral reefs. A variety of gender allocation patterns first described for a number of small tropical serranines (Fischer and Petersen, 1987) only hinted at the great diversity of patterns now being discovered within the Gobiidae. One species whose exceptional range (nearly 3,000 km from northern British Columbia to Baja California Sur: Miller and Lea, 1972) begs for geographic comparison is the blackeye goby; this species has been described as protogynous based solely on data for populations in Barkley Sound, Vancouver Island, British Columbia (Cole, 1983), near the northern limit of its range. The only other detailed study of its reproductive ecology (Breitburg, 1987) in southern California waters demonstrated promiscuous matings and paternal care but assumed that only protogynous sex change occurred. Differences in gender allocation would not be unexpected in species like blackeye goby whose populations span several biogeographic provinces. Geographic studies of gender allocation and the comparative demography of such a species might appreciably clarify our understanding of how variable survivorship under different levels of predation influences gender allocation and mating systems in temperate and tropical reef fishes. Studies of the relations between gender allocation and parental care are generally needed for pomacentrids as well as gobiids.

Also generally lacking are quantitative studies for most aspects of the behavioral ecology of temperate-boreal California fish lineages. For example, the suggestive interrelations among mate choice, sperm competition, and parental care in north Pacific Cottidae have surprisingly been ignored for several decades since the early studies of Patten, Marliave, and DeMartini on eastern north Pacific species in the 1970s, despite numerous studies by Munehara and coworkers on patterns of insemination and fertilization among western North Pacific species in the 1990s. A phylogenetic analysis of the distribution of copulation in eastern as well as western Pacific species of cottids (Munehara, 1999) is needed, as is a description of the patterns of male gonadal investment, including but not limited to data on size-specific testes weights for the entire family. Careful field observations and field and laboratory experiments for select species exhibiting divergent care states and mate pairing could contribute importantly to our understanding of mating and parental care systems in small site-attached fishes. Some obvious examples include intertidal spawners which lack parental care (such as *Oligocottus maculosus* or *Clinocottus analis*) and paternal-caring species with both customary, single-male spawn-tending (e.g., *Artedius fenestralis*) and atypical, group-male egg-tending (*Ascelichthys rhodorus*; DeMartini and Patten, 1979; Petersen et al., 2004).

One group of California marine fishes also has special relevance for studies of the interplay between mate choice and relative maternal and paternal investments in offspring. The syngnathid pipefishes, many of which have long been suspected and have now been shown to be sex reversed (i.e., body-brooding males are the limiting sex and females, not males, are subject to stronger sexual selection), have generated much research interest during the last decade. At least 50 papers on mate choice, sexual selection, and parental investment in syngnathids have appeared in the recent primary literature; the subjects of most of these have been a small group of pipefishes in the northeast Atlantic and Baltic Sea. Several California species such as *Syngnathus californiensis* would provide interesting comparative case studies.

The diel time of spawning and hatching of embryos is almost completely unknown for California reef fishes. Given the ecological differences between tropical and temperate reefs, data on spawning times for the pelagic-spawning tropical derivatives found off southern California (e.g., serranids and labrids) would be instructive, as would comparative data on benthic-spawning tropical derivatives and temperate groups such as the cottids and hexagrammids. Comparisons of populations of garibaldi and other tropical derivatives (such as blacksmith, and especially species with extensive ranges like blackeye goby) from the most temperate to the most tropical extremes of their distribution also would be extremely valuable. Analogous comparative studies would be particularly useful along the east and west coasts of Australia where high levels of species diversity exist along a continuous tropical-temperate gradient.

We conclude this chapter by re-emphasizing the likely great overall influence of upwelling and environmental uncertainty on the reproductive ecology of California's marine fish fauna. While the relatively high incidence of parental care, viviparity, and secondary gonochorism each may have alternative explanations, including or confounded by phylogenetic bias, their coincidence presents a compelling correlation. We hope these patterns will stimulate and help guide future research on the reproductive ecology of fishes in the temperate eastern Pacific and elsewhere.

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Appendix 19.1. Distribution of California and Other Marine Fishes by Reproductive Mode, Gender Allocation and Parental Care Type

This table shows the distribution of reproductive modes (oviparous = ovip, viviparous = vivip), gender allocation (gonochore; or protogynous, protandrous, bidirectional, or simultaneous hermaphrodite), and post-oviposition parental care types (paternal, maternal or biparental) among orders, families, subfamilies or tribes (where variable within family), and species (where variable within subfamilies or tribes) of Californian and major, non-indigenous taxa of marine fishes. Representative species are noted in **bold** type if members of the California fauna. Tropical and other non-California examples are provided in support of tables 19-2 to 19-5. Gonochore-2 refers to secondary gonochore. External body-brooding with parent-embryo nourishment indicated by superscripted asterisk (*).

Taxon (Order, Family or Subfamily)	*Mode*	*Gender Allocation*	*Parental Care*	*Representative Species*	*Key Reference(s)*
Myxiniformes	ovip	gonochore	none		
Myxinidae				***Eptatretus stouti***	Cox 1963; Patzner 1998
Petromyzontiformes	ovip	gonochore	none		
Petromyzontidae				***Lampetra tridentate***	Michael 1984; Russell et al. 1987
Chimaeriformes	ovip	gonochore	none		
Chimaeridae				***Hydrolagus colliei***	Cox 1963
Heterodontiformes	ovip	gonochore	none		
Heterodontidae				***Heterodontus francisci***	Dempster and Herald 1961
Orectolobiformes		gonochore	none		
Rhincodontidae	vivip			***Rhincodon typus***	Joung et al. 1996; Colman 1997
Carcharhiniformes		gonochore	none		
Scyliorhynidae	ovip			***Parmaturus xaniurus***	Cross 1988; Balart et al. 2000
Triakidae	vivip			***Triakis semifasciata***	Kusher et al. 1992
Carcharhinidae	vivip			***Prionace glauca***	Nakano 1994
Lamniformes	vivip	gonochore	none		
Odontaspididae				*Odontaspis taurus*	Gilmore et al. 1983
Alopiidae				***Alopias superciliosus***	Chen et al. 1997
Cetorhinidae				***Cetorhinus maximus***	Matthews 1950
Lamnidae				***Isurus oxyrinchus***	Mollet et al. 2000
Hexanchiformes	vivip	gonochore	none		
Chlamydoselachidae				***Chlamydoselachus anguineus***	Tanaka et al. 1990
Hexanchidae				***Notorynchus cepedianus***	Gilbert 1981; Ebert 1989
Squaliformes	vivip	gonochore	none		
Dalatiidae				***Somniosus pacificus***	Ebert et al. 1987
Squalidae				***Squalus acanthias***	Jones and Geen 1977
Squatiniformes	vivip	gonochore	none		
Squatinidae				***Squatina californica***	Natanson and Cailliet 1986
Rajiformes		gonochore	none		
Torpedinidae	vivip			***Torpedo californica***	Neer and Cailliet 2001
Narcinidae	vivip			***Narcine brasiliensis***	Villavicencio-Garayzar 1993
Rhinobatidae	vivip			***Rhinobatos productus***	Timmons and Bray 1997
Rajidae	ovip			***Raja binoculata***	Zeiner and Wolf 1993
Dasyatidae	vivip			***Dasyatis longa***	Villavicencio et al. 1994
Urolophidae	vivip			***Urolophis halleri***	Babel 1967
Gymnuridae	vivip			***Gymnura marmorata***	Villavicencio-Garayzar 1995
Myliobatidae	vivip			***Myliobatis californica***	Martin and Cailliet 1988
Mobulinae	vivip			***Manta birostris***	Yano et al. 1999
Acipenseriformes	ovip	gonochore	none		
Acipenseridae				***Acipenser transmontanus***	Chapman et al. 1996
Elopiformes	ovip	gonochore	none		
Elopidae				***Elops affinis***	none
Megalopidae				*Megalops atlanticus*	Crabtree et al. 1997a
Albuliformes	ovip	gonochore	none		
Albulidae				***Albula vulpes***	Crabtree et al. 1997b
Anguilliformes	ovip		none		
Muraenidae		protogynous		*Gymnothorax fimbriata*	Fishelson 1992
		simultaneous		*Sideria spp*	Fishelson 1992
		protandrous		*Rhinomuraena quaesita*	Shen et al. 1979
		gonochore		*Gymnothorax meleagris*	Fishelson 1992
Ophichthidae		gonochore		*Ophichthus rufus*	Casadevall et al. 2001
Derichthyidae		?		***Derichthys serpentinus***	none

Appendix 19.1. (continued)

Taxon (Order, Family or Subfamily)	*Mode*	*Gender Allocation*	*Parental Care*	*Representative Species*	*Key Reference(s)*
Congridae		gonochore		*Gnathophis spp*	Fishelson 1994
Nettastomatidae		?		***Venefica tentaculata***	none
Serrivomeridae		?		***Serrivomer sector***	none
Nemichthyidae		gonochore		***Nemichthys scolopaceus***	Fishelson 1994
Saccopharyngiformes	ovip	?	none		
Cyematidae				***Cyema atrum***	none
Saccopharyngidae				***Saccopharynx lavenbergi***	none
Eurypharyngidae				***Eurypharynx pelecanoides***	none
Clupeiformes	ovip	gonochore	none		
Clupeidae				***Opisthonema libertate***	Torres-Villegas and Perez-Gomez 1988
Engraulidae				***Anchoa spp***	Caddell 1988
Gonorhynchiformes	ovip	gonochore	none		
Chanidae				***Chanos chanos***	Delsman 1929
Siluriformes	ovip	gonochore			
Ariidae			paternal	*Arius graeffei*	Rimmer 1985a, b
Plotosidae			paternal	*Plotosus lineatus*	Thresher 1984
Osmeriformes	ovip	gonochore	none		
Argentinidae				***Argentina sialis***	Bergstad 1993
Microstomidae				***Nansenia crassa***	none
Bathylagidae				***Bathylagus ochotensis***	Miya 1995
Opisthoproctidae				*Opisthoproctus soleatus*	Alekseyev et al. 1982
Alepocephalidae				*Alepocephalus bairdii*	Allain 1999
Platytroctidae				***Sagamichthys abei***	none
Osmeridae				***Hypomesus pretiosus***	Middaugh et al. 1987
Salmoniformes	ovip				
Salmonidae		gonochore	maternal	***Oncorhynchus nerka***	McPhee and Quinn 1998
Stomiiformes	ovip		none		
Gonostomatidae		protandry		*Cyclothone atraria*	Miya and Nemoto 1991
Sternoptychidae		?		*Sternoptyx diaphana*	Baird et al. 1990
Phosichthyidae		?		*Vinciguerria nimbaria*	Tomas and Panfili 2000
Stomiidae		?		***Chauliodus macouni***	none
Giganturidae		?		***Gigantura indica***	none
Aulopiformes	ovip		none		
Scopelarchidae		simultaneous		*Benthalbella infans*	Merrett et al. 1973
Notosudidae		?simultaneous		***Scopelosaurus spp***	none
Synodontidae		gonochore		*Synodus spp*	Zaiser and Moyer 1981; Donaldson 1990
Paralepididae		simultaneous		*Lestidium pseudosphyraenoides*	Mead et al. 1964
Anotopteridae		?simultaneous		***Anotopterus pharao***	none
Alepisauridae		simultaneous		***Alepisaurus ferox***	Mead 1960; Smith and Atz 1973
Myctophiformes	ovip		none		
Neoscopelidae				***Scopelengys tristis***	none
Myctophidae		gonochore		***Stenobrachius leucopsaurus***	Childress et al. 1980
Lampridiformes	ovip	?gonochore	none		
Lampridae				***Lampris guttata***	none
Lophotidae				***Lophotus lacepede***	none
Trachipteridae				***Zu cristatus***	Olney and Naplin 1980
Regalecidae				***Regalecus glesne***	Montero et al. 1995
Ophidiiformes		gonochore	none		
Carapidae				*Carapus spp*	none
Ophidiidae	ovip			*Ophidion barbatum*	Breder and Rosen 1966
Bythitidae	vivip			***Brosmophycis marginata***	Hart 1973
Gadiformes	ovip	gonochore	none		
Moridae				*Antimora rostrata*	Jakobsdottir and Magnusson 2001
Melanonidae				***Melanonus zugmayeri***	none
Macrouridae				***Coryphaenoides spp***	Stein and Pearcy 1982
Bregmacerotidae				*Bregmaceros atlanticus*	Clancey 1956
Merlucciidae				***Merluccius productus***	McFarlane and Saunders 1997
Gadidae				***Theragra chalcogramma***	Hinckley 1987

Appendix 19.1. (continued)

Taxon (Order, Family or Subfamily)	*Mode*	*Gender Allocation*	*Parental Care*	*Representative Species*	*Key Reference(s)*
Batrachoidiformes	ovip				
Batrachoididae		gonochore	paternal	***Porichthys notatus***	DeMartini 1988b, 1990; Brantley and Bass 1994
Lophiiformes	ovip				
Lophiidae		gonochore		***Lophiomus setigerus***	Yoneda et al. 1997, 1998
Antennariidae		gonochore	none	*Antennarius striatus*	Pietsch and Grobecker 1987
			paternal	*Lophiocharon trisignatus*	Pietsch and Grobecker 1987
Ogcocephalidae		?gonochore	?none	***Zalieutes elater***	none
Caulophrynidae		gonochore	none	*Caulophryne spp* ***(jordani)***	Pietsch 1976
Melanocetidae		gonochore	none	*Melanocetus spp* ***(johnsonii)***	Pietsch 1976
Oneirodidae		gonochore	none	*Oneirodes spp* ***(acanthias)***	Pietsch 1976
Ceratiidae		gonochore	none	***Cryptopsaras couesii***	Pietsch 1976
Gigantactinidae		gonochore	none	*Gigantactis spp* ***(macronema)***	Pietsch 1976
Linophrynidae		gonochore	none	*Linophryne spp* ***(coronata)***	Pietsch 1976
Mugiliformes	ovip	gonochore	none		
Mugilidae				***Mugil cephalus***	Greeley et al. 1987
Atheriniformes	ovip	gonochore			
Atherinidae			none	***Leuresthes tenuis***	Griem and Martin 2000
Beloniformes		gonochore	none		
Belonidae	ovip			***Strongylura exilis***	Ambrose and Moser 1988
Scomberesocidae	ovip			***Cololabis saira***	Kosaka 2000
Exocoetidae	ovip			***Cheilopogon heterurus***	Dasilao et al. 1998; Ichimaru and Nakazono 1999
Hemiramphidae	ovip			*Hyporhamphus unifasciatus*	Durai et al. 1988
Cyprinodontiformes	ovip	gonochore			
Fundulidae			none	*Fundulus heteroclitus*	Able 1984
Stephanoberyciformes	ovip	gonochore	none		
Melamphaeidae				***Scopelogadus mizolepis***	Keene et al. 1987; Andrianov and Bekker 1989; Ebeling and Weed 1963
Rondeletiidae				***Rondeletia loricata***	none
Cetomimidae				***Cetomimus sp***	none
Beryciformes	ovip	gonochore	none		
Anoplogastridae				***Anoplogaster cornuta***	none
Anomalopidae				*Phthanophaneron harveyi*	none
Trachichthyidae				*Hoplostethus atlanticus*	Clark et al. 1994
Berycidae				*Beryx splendens*	Lehodey et al. 1997
Holocentridae				*Myripristis amaena*	Dee and Parrish 1994
Zeiformes	ovip	gonochore	none		
Zeidae				***Zenopsis nebulosus***	Parin et al. 1988
Oreosomatidae				***Allocyttus verrucosus***	Lyle and Smith 1997
Gasterosteiformes	ovip	gonochore			
Aulorhynchidae			paternal	***Aulorhynchus flavidus***	Marliave 1976
Gasterosteidae			paternal	***Gasterosteus aculeatus***	Wootton 1984
Pegasidae			none	*Eurypegasus draconis*	Herold and Clark 1993
Solenostomidae			maternal*	*Solenostomus spp*	Wetzel and Wourms 1995
Syngnathidae			paternal*	*Syngnathus fuscus*	Campbell and Able 1998
Aulostomidae			none	*Aulostomus chinensis*	Thresher 1984
Fistulariidae			none	***Fistularia commersonii***	Delsman 1921; Watson and Leis 1974
Macroramphosidae			none	***Macroramphosus gracilis***	Arruda 1988
Scorpaeniformes					
Dactylopteridae	ovip	gonochore	none	*Dactylopterus volitans*	none
Scorpaenidae		gonochore	none		
Sebastinae	vivip			***Sebastes flavidus***	Hopkins et al. 1995
	vivip			*Sebastes schlegelii*	Boehlert et al. 1986
Scorpaeninae	ovip			***Scorpaena guttata***	Orton 1955
Sebastolobinae	ovip			***Sebastolobus alascanus***	Erickson and Pikitch 1993
Caracanthidae	ovip	?protogynous	none	*Caracanthus spp*	Cole 2003
Triglidae	ovip	gonochore	none	*Prionotus evolans*	McBride and Able 1994

Appendix 19.1. (continued)

Taxon (Order, Family or Subfamily)	*Mode*	*Gender Allocation*	*Parental Care*	*Representative Species*	*Key Reference(s)*
Platycephalidae	ovip	protandrous	none	*Inegocia japonica*	Fujii 1971
	ovip	gonochore-2	none	*Platycephalus speculator*	Hyndes et al. 1992
Anoplomatidae	ovip	gonochore	none	***Anoplopoma fimbria***	Hunter et al. 1989
Hexagrammidae	ovip	gonochore	paternal	***Oxylebius pictus***	DeMartini and Anderson 1980
Rhamphocottidae	ovip	gonochore	paternal	***Rhamphocottus richardsoni***	Munehara et al. 1999
Cottidae	ovip	gonochore	paternal	***Scorpaenichthys marmoratus***	Lauth 1989
			maternal	***Hemilepidotus hemilepidotus***	DeMartini and Patten 1979
			none	***Clinocottus acuticeps***	Marliave 1981b
Hemitripteridae	ovip	gonochore	none	*Hemitripterus villosus*	Munehara et al. 1997
Psychrolutidae	ovip	gonochore	paternal	*Gilbertidia sigalutes;*	Marliave 1981a;
				Psychrolutes phrictus	Drazen et al. 2003
Agonidae	ovip	gonochore	none	***Podothecus sachi***	Munehara 1997
Cyclopteridae	ovip	gonochore	paternal	***Eumicrotremus orbis***	Able et al. 1984; Matarese et al. 1989
Liparidae	ovip	gonochore	paternal	***Liparis fucensis***	DeMartini 1978
			none	***Careproctus spp***	Somerton and Donaldson 1998
Perciformes					
Centropomidae	ovip	protandrous	none	*Centropomis undecimalis*	Taylor et al. 2000
Moronidae	ovip	gonochore	none	***Morone saxatilis***	Scofield 1931; Woodhull 1947
Polyprionidae	ovip	gonochore	none	*Polyprion americanus*	Peres and Klippel 2003
Howellidae	ovip	?gonochore	none	***Howella sp***	none
Serranidae	ovip		none		
Serraninae			none		
Diplectrum spp		simultaneous		***Diplectrum pacificum***	Bortone 1977
Serranus spp		simultaneous		*Serranus tabacarius*	Petersen 1995
		protogynous		*Serranus fasciatus*	Petersen 1990a
Paralabrax spp		protogynous		***Paralabrax maculatofasciatus***	Hastings 1989; Hovey and Allen 2000
		gonochore-2		***Paralabrax clathratus***	Smith and Young 1966; Oda et al. 1993
Anthiinae		protogynous	none	*Hypoplectrodes maccullochi*	Webb and Kingsford 1992
Epinephelinae	ovip	protogynous	none	*Epinephelus guttatus*	Shapiro et al. 1994
		gonochore-2		*Epinephelus striatus*	Sadovy and Colin 1995
tr. Grammistini	ovip	protogynous	none	*Rypticus spp*	Smith 1965
Pseudochromidae	ovip	?gonochore-2	paternal	*Pseudochromis olivaceus*	Fishelson 1989; Thresher 1984
Grammatidae	ovip	gonochore-2	paternal	*Gramma loreto*	Asoh and Yoshikawa 1996; Shapiro 1997
Plesiopidae	ovip	?gonochore-2	paternal	*Plesiops nigricans*	Fishelson 1989; Thresher 1984
Opistognathidae	ovip	gonochore	paternal	*Opistognathus aurifrons*	Hess 1993
Priacanthidae	ovip	?gonochore	none	*Heteropriacanthus cruentatus*	Colin and Clavijo 1978
Apogonidae	ovip	gonochore	paternal	*Apogon lineatus*	Kume et al. 2000
Malacanthidae	ovip	?protogynous	none	***Caulolatilus princeps***	Elorduy-Garay and Ramirez-Luna 1994
Pomatomidae	ovip	gonochore	none	*Pomatomus saltatrix*	Conand 1975
Nematistiidae	ovip	?gonochore	none	***Nematistius pectoralis***	none
Echeneidae	ovip	gonochore	none	***Remora osteochir***	Morota and Fujita 1995
Rachycentridae	ovip	gonochore	none	*Rachycentron canadensis*	Brown-Peterson et al. 2001
Coryphaenidae	ovip	gonochore	none	***Coryphaena hippurus***	Oxenford 1999
Carangidae	ovip	gonochore	none	***Trachurus symmetricus***	Macewicz and Hunter 1993
Leiognathidae	ovip	gonochore	none	*Leiognathus brevirostris*	Jayawardane and Dayaratne 1998
Bramidae	ovip	gonochore	none	***Brama japonica***	Yoon and Shimazaki 1981
Caristiidae	ovip	?gonochore	none	***Caristius macropus***	none
Lutjanidae	ovip	gonochore	none	*Lutjanus spp*	Grimes 1987
Caesionidae	ovip	gonochore	none	*Pterocaesio diagramma*	Choi et al. 1996
Lobotidae	ovip	?	none	***Lobotes surinamensis***	none
Gerreidae	ovip	gonochore	none	***Gerres cinereus***	Baez and Alvarez-Lajonchere 1983
Haemulidae	ovip	gonochore	none	*Haemulon sciurus*	Garcia-Cagide 1986
Sparidae	ovip	protogynous	none	***Calamus brachysomus***	Druzhinin 1976
		protandrous		*Lithognathus mormyrus*	Besseau and Brusle-Sicard 1995
		gonochore-2		*Diplodus sargus*	Buxton and Garratt 1990
Lethrinidae	ovip	protogynous	none	*Lethrinus miniatus*	Bean et al. 2003

Appendix 19.1. (continued)

Taxon (Order, Family or Subfamily)	Mode	Gender Allocation	Parental Care	Representative Species	Key Reference(s)
Nemipteridae	ovip	protogynous	none	*Scolopsis spp*	Young and Martin 1985
		gonochore-2	none	*Nemipterus virgatus*	Lau and Sadovy 2001
Polynemidae	ovip	protandrous	none	*Polydactylus sexfilis*	Szyper et al. 1991
Sciaenidae	ovip	gonochore	none	***Seriphus politus***	DeMartini 1991
Mullidae	ovip	gonochore	none	*Pseudupeneus maculatus*	Colin and Clavijo 1978
Pempheridae	ovip	gonochore	none	*Pempheris vanicolensis*	Golani and Diamant 1991
Chaetodontidae	ovip	gonochore	none	*Chaetodon spp*	Hourigan 1984, 1989
Pomacanthidae	ovip	gonochore	none	*Centropyge, Pomacanthus spp*	Sakai 1997
Pentacerotidae	ovip	gonochore	none	***Pseudopentaceros wheeleri***	Yanagimoto and Humphreys unpubl
Kyphosidae	ovip	gonochore	none		
Girellinae				*Girella tricuspidata*	Pollock 1981
Kyphosinae				*Scorpis lineolata*	Dedual and Pankhurst 1992
Teraponidae	ovip	?gonochore	none	*Terapon jarbua*	none
Kuhliidae	ovip	?gonochore	none	*Kuhlia sandwichiensis*	Tester and Takata 1953
Cirrhitidae	ovip	protogynous	none	*Neocirrhites armatus*	Sadovy and Donaldson 1995
		bidirectional	none	*Cirrhitichthys aureus*	Kobayashi and Suzuki 1992
Cheilodactylidae	ovip	gonochore	none	*Cheilodactylus spectabilis*	McCormick 1989
Cepolidae	ovip	gonochore	none	*Cepola rubescens*	Sergiou et al. 1996
Cichlidae	ovip	gonochore	biparental	***Tilapia zillii***	El-Zarka 1956; Loiselle 1977
Embiotocidae	vivip	gonochore	none	***Embiotoca jacksoni***	Baltz 1984
Pomacentridae	ovip	protandrous			
Amphiprioninae			paternal	*Amphiprion melanopus*	Ross 1978
			biparental	*Amphiprion clarkii*	Moyer and Bell 1976
Pomacentrinae		gonochore	paternal	***Hypsypops rubicundus***	Clarke 1970; DeMartini et al. 1994
Dascyllus spp		protogynous	paternal	*Dascyllus albisella*	Godwin 1995; Asoh et al. 2001
Labridae	ovip	protogynous	none	***Semicossyphus pulcher***	Warner 1975a; Cowen 1990
		gonochore-2	none	***Oxyjulis californica***	Diener 1976
			paternal	*Symphodus ocellatus*	Warner and Lejeune 1985
Scaridae	ovip	protogynous	none	*Scarus spp, Nicholsina spp*	Robertson et al. 1982
		gonochore	none	*Leptoscarus vaigiensis*	Robertson et al. 1982
Pinguipedidae	ovip	protogynous	none	*Parapercis snyderi*	Kobayashi et al. 1993
Bathymasteridae	ovip	?gonochore	paternal	***Rathbunella hypoplecta***	Fitch and Lavenberg 1975
Zoarcidae		gonochore			
Zoarces spp	vivip		none	*Zoarces elongatus*	Koya et al. 1995
other genera	ovip		?biparentl	***Lycodopsis pacificus***	Levings 1969
Stichaeidae	ovip	gonochore	paternal	***Xiphister atropurpureus***	Marliave and DeMartini 1977
	ovip		maternal	***Anoplarchus purpurescens***	Coleman 1992
Cryptacanthodidae	ovip	?gonochore	?	*Cryptacanthodes bergi*	Shiogaki 1982
Pholidae	ovip	gonochore	biparental	***Pholis laeta***	Hughes 1986
Anarhichadidae	ovip	?	biparental	***Anarrhichthys ocellatus***	Marliave 1987
Ptilichthyidae	ovip	?	?	*Ptilichthys goodei*	none
Zaproridae	ovip	?	?none	***Zaprora silenus***	Fitch and Lavenberg 1971
Scytalinidae	ovip	gonochore	?	***Scytalina cerdale***	none
Chiasmodontidae	ovip	?	?none	***Chiasmodon niger***	none
Trichodontidae	ovip	?gonochore	none	***Trichodon trichodon***	Marliave 1981c; Okiyama 1990
Trichonotidae	ovip	protogynous	none	*Trichonotus filamentosus*	Kusen et al. 1991
Creediidae	ovip	protandrous	?none	*Crystallodytes cookei*	Langston 2003
		gonochore		*Apodocreedia vanderholsti*	
Ammodytidae	ovip	?gonochore	none	***Ammodytes hexapterus***	Robards et al. 1999
Trachinidae	ovip	gonochore	?none	*Trachinus vipera*	none
Uranoscopidae	ovip	?gonochore	?none	*Uranoscopus scaber*	Boundka et al. 1998
Tripterygiidae	ovip	gonochore	paternal	***Axoclinus carminalis***	Petersen 1989
Dactyloscopidae	ovip	gonochore	paternal	*Dactyloscopus spp*	Dawson 1982
Labrisomidae	ovip	gonochore	paternal	***Malacoctenus hubbsi***	Petersen 1988
	vivip		none	*Starksia hoesii*	Rosenblatt and Taylor 1971
Clinidae		gonochore			
Myxodini	ovip		paternal	***Heterostichus rostratus***	Coyer 1982
Ophiclinini	vivip		none	*Ophiclinus spp*	George and Springer 1980
Clinini	vivip		none	*Heteroclinus spp*	Gunn and Thresher 1991
Chaenopsidae	ovip	?gonochore	paternal	*Emblemaria hypacanthus*	Hastings 1992
Blenniidae	ovip	gonochore	paternal	***Hypsoblennius spp***	Stephens et al. 1970

Appendix 19.1. (continued)

Taxon (Order, Family or Subfamily)	*Mode*	*Gender Allocation*	*Parental Care*	*Representative Species*	*Key Reference(s)*
Icosteidae	ovip	?	none	***Icosteus aenigmaticus***	Fitch and Lavenberg 1971
Gobiesocidae	ovip	gonochore	paternal	***Gobiesox maeandricus***	Marliave and DeMartini 1977
Callionymidae	ovip	gonochore	none	*Diplogrammus pauciradiatus*	Harrington 1997
Eleotridae	ovip	?gonochore	paternal	*Gobiomorphus breviceps*	Hamilton and Poulin 1999
Gobiidae	ovip	protogynous	paternal	***Rhinogobiops nicholsii***	Ebert and Turner 1962; Cole 1983
		bidirectional	paternal	***Lythrypnus spp***	St. Mary 2000
		simultaneous	paternal	***Lythrypnus spp***	St. Mary 2000
		gonochore	biparental	***Clevelandia ios***	Brothers 1975
		gonochore	?paternal	***Typhlogobius californiensis***	MacGinitie 1939
Microdesmidae	ovip	?	none	*Gunnellichthys spp*	none
Ephippidae	ovip	gonochore	none	***Chaetodipterus zonatus***	Martinez-Pechero et al. 1990
Siganidae	ovip	gonochore	none	*Siganus canaliculatus*	El-Sayed and Bary 1994
Luvaridae	ovip	?		***Luvarus imperialis***	Nishikawa 1987
Zanclidae	ovip	?gonochore	none	*Zanclus cornutus*	none
Acanthuridae	ovip	gonochore	none	*Acanthurus nigrofuscus*	Myrberg et al. 1988
Sphyraenidae	ovip	gonochore	none	***Sphyraena argentea***	Walford 1932
Gempylidae	ovip	gonochore	none	***Thyrsites atun***	Griffiths 2002
Trichiuridae	ovip	?	none	*Lepidopus caudatus*	Demestre et al. 1993
Scombridae	ovip	gonochore	none	***Thunnus albacares***	Schaefer 1998
Xiphiidae	ovip	gonochore	none		
Xiphiinae				***Xiphias gladius***	DeMartini et al. 2000
Istiophorinae				***Istiophorus spp***	DeSylva and Breder 1997
Centrolophidae	ovip	?		*Hyperoglyphe antarctica*	Baelde 1996
Nomeidae	ovip	?	none	*Cubiceps gracilis*	none
Tetragonuridae	ovip	?	none	*Tetragonurus spp*	none
Stromateidae	ovip	gonochore	none	***Peprilus simillimus***	Goldberg 1981b
Pleuronectiformes	ovip	gonochore	none		
Bothidae				***Bothus constellatus***	Tapia-Garcia et al. 2000
Paralichthyidae				***Citharichthys spp***	Goldberg and Pham 1987
Pleuronectidae				***Microstomus pacificus***	Hunter et al. 1992
Achiridae				***Achirus mazatlanus***	Amezcua-Linares et al. 1992
Cynoglossidae				***Symphurus atricaudus***	Goldberg 1981a
Tetraodontiformes	ovip				
Balistidae		gonochore			
			maternal	***Balistes polylepis***	Strand 1978
			biparental	*Pseudobalistes flavimarginatus*	Gladstone 1994
Monacanthidae		?	none	*Oxymonacanthus longirostris*	Kokita and Nakazono 2001
			biparental	*Paramonacanthus japonicus*	Nakazono and Kawase 1993
Ostraciidae		?protogynous	?none	*Ostracion meleagris*	Moyer 1979; Leis and Moyer 1985
Tetraodontidae		?	none	*Canthigaster rostrata*	Sikkel 1990
Diodontidae		?	none	***Diodon holacanthus***	Sakamoto and Suzuki 1978
Molidae		?	none	***Mola mola***	none