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Maternal size effects on early life traits of the temperate fish *Symphodus roissali*

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ABSTRACT: The relative importance of maternal influences and time of reproduction on early life-history traits in the temperate five-spotted wrasse *Symphodus roissali* was examined. On 5 occasions during the reproductive period, groups of 4 small and 4 large females were collected and their eggs were fertilized with milt from 1 male. This multiple female fertilization experiment allowed the evaluation and comparison of potential contribution of maternal size on the following early life traits of progeny: egg properties (diameter and dry weight) and larval properties (larval length and dry weight). Large females (>9 cm) produced larger eggs and larvae than did small females (<9 cm). The differences in progeny properties between both size groups of females were maintained throughout the reproductive period, with increasing variations in larval length at the end. As juvenile survival of *S. roissali* is affected by larval size at hatching and this is, in turn, affected by maternal size and time of spawning, it can be concluded that the size of females plays a major role in reproductive success, with larger females maximizing the survival of the young.

KEY WORDS: Female size · Egg size · Early life history traits · *Symphodus roissali*

INTRODUCTION

Population dynamics of marine fishes are characterized by high larval mortality (Werner & Fuiman 2002), which is predominantly driven by size- and growth-selective processes (Meekan & Fortier 1996). Size at hatching and growth rate strongly influence survival before and after settlement (Meekan & Fortier 1996), with higher survival in juveniles from large larvae (Houde 1994, Bergenius et al. 2002, Shima & Findlay 2002, Tomkiewicz et al. 2003, Raventos & Macpherson 2005). Moreover, predation and starvation are major factors at the larval stage (Houde 1987), and changes in morphological traits can strongly influence larval survival. Search for prey and avoidance of predation are strongly related to swimming capabilities, which, in turn, depend on the size and condition of larvae (Houde 1987, Blaxter 1988, Leis & Carson-Ewart 2001). However, the seminal causes of variation in larval size and growth are poorly understood. Variations in early life traits and growth rates have been mainly related to parental influences and environmental fluctuations (Green & McCormick 2005). Environmental factors encompass the physical and biotic processes acting on developing eggs and larvae, including the physicochemical conditions of the water and food availability among others (Chambers 1997). Maternal influences due to nutritional provisioning of the embryo (Bernardo 1996) are assumed to predominate over paternal contribution, as sperm contain virtually no extra-nuclear material. From fertilization of the egg to the onset of feeding in the plankton, larvae are dependent on the energy reserves within the yolk (reviewed by Love 1980). Finally, the embryo reserve is a direct result of the reserves the female is able to mobilize during oogenesis and maturation of oocytes (Kerrigan 1997).

In marine fish, maternal size effects have been demonstrated on egg and larval size (Hay 1985, Panagiotaki & Geffen 1992, Chambers & Leggett 1996, Marteinsdottir & Steinarsson 1998, Green & McCormick 2005), as well as on egg and larval dry weight at hatching (Green & McCormick 2005). Most sources, includ-

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ing some the most recent ones, have documented positive relationships between maternal size on the one hand and egg and larval size on the other (Kamler 2005), but a few others reported no clear relationship (reviewed in Kamler 1992, Chambers 1997). Moreover, variability in egg size may also be a result of a bet-hedging strategy, in order to face unpredictable environmental conditions (Koops et al. 2003, Einum & Fleming 2004). The spawning strategy of females can be a contributing factor confusing this relationship: asynchronous spawning activity or batch sequence within a reproductive season can contribute to egg size variation between successive batches (Marteinsdottir & Steinarsson 1998, Tamada & Iwata 2005). The variation of any early life-history trait can be related to female condition, which, in turn, can be coupled to the decreasing condition of the female as the spawning season advances (Chambers & Waiwood 1996).

The present study experimentally examined the relative importance of maternal influences on early life-history traits in the temperate five-spotted wrasse *Symphodus roissali*—a multiple spawning marine fish with paternal egg care consisting of nest construction, guarding and fanning of the eggs until they hatch (Lejeune 1985). A factorial design with size class of females and time of the reproduction period as factors allowed the evaluation and comparison of potential maternal contribution on five-spotted wrasse early life traits: egg diameter and dry weight, and larval length and dry weight at hatching.

MATERIALS AND METHODS

Study species. The five-spotted wrasse *Symphodus roissali* is a small (<15 cm) endemic Mediterranean wrasse (Quignard & Pras 1986) inhabiting shallow rocky bottoms (<6 m) (Helas et al. 1982). On NW Mediterranean coasts, *S. roissali* mating activity usually begins at the end of March and ends in mid-June, depending on the water temperature (Lejeune 1985). Over the course of the spawning season, primary (nesting) males build and guard several nests consecutively. While females are sexually active, they continuously visit nests and may lay several benthic clutches during each visit (Lejeune 1985). There are no differences in spawning rates among female size classes (Warner & Lejeune 1985). Secondary males sometimes sneak into nests and fertilize clutches (Lejeune 1985). Duration of the planktonic larval phase is short, lasting between 11 and 14 d (Raventos & Macpherson 2001), and larvae stay nearshore (Sabatés et al. 2003). Settlement always occurs on branching algae at depths shallower than 8 m (García-Rubies & Macpherson 1995) when individuals reach about 5 to 7 mm (Raventos & Macpherson 2001).

Symphodus roissali is a particularly good candidate to test maternal effects since, in a previous study, Raventos & Macpherson (2005) demonstrated that recruitment survival is higher in those individuals with a larger size at hatching. Therefore, analyzing the relationship between maternal size and size at hatching will enable us to examine the effects of maternal size on recruitment success.

Field work and parental selection. Observations by SCUBA diving began at the end of February in order to determine the start of the reproduction period. The reproduction period was considered to have begun when the primary males of the population displayed fighting behavior. Nesting activity and spawning in the field began in mid-April, which was interrupted by sea storms, and continued until the beginning of June. The deleterious effects of wave height on nesting activities have previously been demonstrated (Raventos 2004). Unusually high temperatures were recorded in the Mediterranean Sea in 2006, which shortened the reproduction period to about 1.5 mo (Raventos 2004).

Mature individuals were collected from the wild within the same bay (<1 ha) throughout the experimental process. On 5 occasions throughout the reproductive period, 4 small females and 4 large females (see Table 1 for details) were collected and 1 male randomly picked (size in Table 1) and brought to the laboratory. On each of the 5 sampling occasions, eggs from all 8 females were fertilized with an equal amount of sperm from the same male. All 8 females and the male were different individuals on each of the 5 sampling occasions. A total of 54 individuals (47 females and 7 males) was collected and mated as shown in Table 1.

Aquarium experiments. Within 2 h of collection, 3 clutches of eggs were hand stripped from each female (n = 4 small and 4 large females, 5 trials). One was placed in a 0.5 ml vial and frozen at –80°C for subsequent dry weight analysis. The other 2 clutches were placed in small Petri dishes. Parental maintenance of the embryos through ventilation was supplied by additional air pumps, in order to limit the fanning rate effect (Mills & Reynolds 2002, Green et al. 2006). Eggs attached naturally to the bottom of the Petri dishes because of the sticky properties of the chorion. One of the clutches was used immediately for egg measurement, and the last clutch was kept for *in vitro* fertilization. Fertilization was performed with milt from a single male, in order to limit the amount of variation due to paternal influences. Fertilized eggs were stored in 5 l containers in a constant temperature room (19°C) at a salinity of 37.7, under a natural photoperiod (12 h light:12 h dark) and with additional air to supply the fanning activity of the male. The containers were checked every day, and the experiment was terminated when the larvae hatched overnight. Of all the

Table 1. *Symphodus roissali*. Time of sampling, size of parental fish and number of progeny used in the experimental trials. Size in cm

Trial	Sampling date	Female size Small (Mean ± SE)	Female size Large (Mean ± SE)	Male size	No. of eggs measured for diameter	No. of eggs dry weighed	No. of larvae measured	No. of larvae dry weighed
1	28 Apr	6.6 ± 0.3	10.3 ± 0.8	10.8	141	28	57	29
2	11 May	7.3 ± 0.7	10.8 ± 0.4	10	127	30	59	29
3	19 May	7.1 ± 0.2	10.9 ± 0.4	11	146	29	–	–
4	26 May	6.7 ± 0.2	10.1 ± 0.8	9.5	139	30	58	30
5	2 Jun	7.3 ± 0.3	10.6 ± 0.3	12	146	26	59	27

larvae present in the tank, 10 were collected the next morning and their size was measured, and another subsample was ultrafrozen for measurements of dry weight. The total number of eggs and larvae used in each of the 5 experimental trials is shown in Table 1. Only 4 complete trials (eggs and larvae from at least 3 females of each size group) could be performed, because eggs from Trial 3 were not viable for unknown reasons, and consequently, no larvae were obtained in this trial (see Table 1).

Early life trait measurements. The diameter of a total of 699 eggs was measured and 143 were dry weighed (see Table 1). Diameter of the fresh, spherical and unfertilized eggs was measured to the nearest 0.01 mm by image analysis (Zeiss binocular, Progress camera and software) within 1 h after stripping. The additional ultrafrozen (–80°C) duplicate samples of eggs from each female were taken for measurements of dry weight. After defrosting (which did not break the eggs), excess seawater was removed, and individual eggs were transferred to a preweighed aluminum cup and placed for 24 h at 60°C in a desiccator. Dry weight was obtained to 1.0 µg precision using a Perkin-Elmer AD-4 autobalance.

Of the 233 larvae taken for size measurements, 101 were ultrafrozen (–80°C) and dry weighed (see Table 1). Within the morning of hatching, larvae were randomly caught and slightly anaesthetized with clove oil for photographing. After calibration with a standard, the total length (L_T, mm) could be measured directly by image analysis (Zeiss binocular, Progress camera and software). The additional ultrafrozen samples of larvae were weighed following the same methodologies as for eggs.

Statistical analysis. Differences in early life traits among size classes of females and between different times during the reproductive period were compared using 2-way analyses of variance (ANOVA), considering class size and time as fixed factors. Our unit of replication was the clutch itself (for egg measurements) or the incubation tank where progeny of a single female were incubated (for larval measurements). For all data, the fundamental assumptions for ANOVA were tested.

RESULTS

Egg diameter

Average egg diameter was 725 µm (range from 660 to 795 µm). Average egg size tended to decrease as the season progressed for both size classes of females ($r^2 = 0.31$ and 0.33 for large and small females, respectively). The 2-way ANOVA showed a significant effect of time ($F_{4,20} = 17.2$, $p < 0.001$) and female type ($F_{1,20} = 29.1$, $p < 0.001$) on egg size (Fig. 1). Females produced larger eggs at the beginning of the reproduction period and larger females produced larger eggs than smaller females throughout the reproduction period (Tukey test, $p < 0.05$)

Egg dry weight

Average dry weight was 0.048 µg (range from 0.38 to 0.60 µg). Only time had a significant effect ($F_{4,20} = 5.7$, $p < 0.01$) on the egg dry weight, with no clear trends in the post hoc analysis. The coefficient of variation (CV = 100 × standard deviation/mean) for the

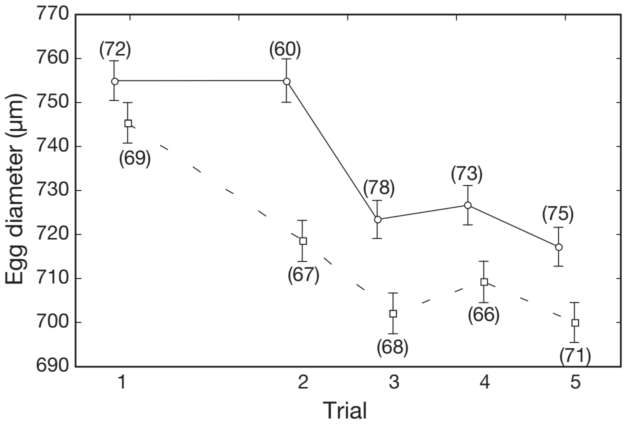

Fig. 1. *Symphodus roissali*. Diameter (±SE) of eggs throughout the reproductive season. ——: averaged values for large females (>9 cm); – – – –: averaged values for small females (<9 cm); numbers in parentheses: sample size

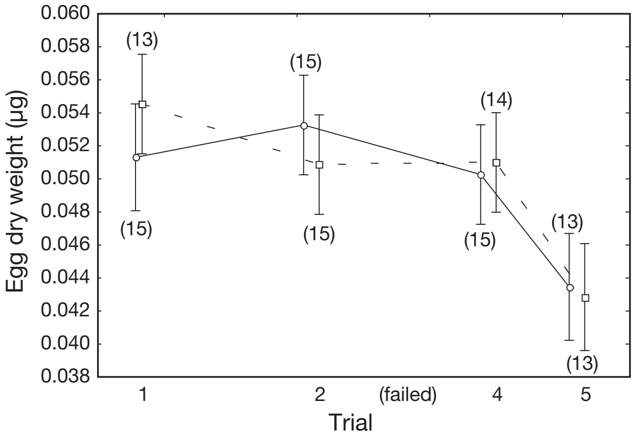

Fig. 2. *Symphodus roissali*. Egg dry weight (±SE) over the reproductive period, excluding Trial 3. ——: averaged values for large females (>9 cm); – – – –: averaged values for small females (<9 cm); numbers in parentheses: sample size

weight data was high at 14.3%, especially when compared to that of egg diameter (CV = 3.7%). When eggs from Trial 3 were excluded from the analysis (because, for unknown reasons, they were not viable), the post hoc analysis revealed a more clearly seasonal trend with a significant difference between the egg dry weights from the end of the season and those from the rest of the reproductive period (Fig. 2) (Tukey test, $p < 0.05$).

Larval length

Average larval length was 3.11 mm (range from 2.85 to 3.38 mm). Females produced larger larvae at the beginning of the reproduction period ($F_{3,16} = 13.7$, $p < 0.001$) and larger females produced larger larvae throughout the reproductive period ($F_{1,16} = 19.2$, $p < 0.001$; Tukey test, $p < 0.05$) (Fig. 3). The difference between larval sizes from the 2 female size groups was larger at the end than at the beginning of the reproductive period (Fig. 3).

Larval dry weight

Average larval dry weight was 0.019 µg (range from 0.012 to 0.031 µg). Only time had a significant effect ($F_{3,16} = 3.6$, $p < 0.01$) on the larval dry weight based on the post hoc analysis; only larvae from the first batch were heavier than the rest (Fig. 4).

DISCUSSION

The results of the present study demonstrate a significant positive relationship between maternal size and egg and larval size. Furthermore, maternal size and time during the reproductive period explained a large proportion of the variation in offspring size in *Symphodus roissali*. Maternal size influence was apparent in egg sizes prior to fertilization, and its effects were maintained throughout the reproductive period, with increasing variation between size classes at the end.

Within the 30 clutches resulting from the trials throughout the experimental process, differences in egg size were more closely related to time than female class size; however, significant differences between female size groups were maintained throughout the reproduction period. Maternal size effects on egg size have been reported for a number of marine and freshwater fish species (Blaxter & Hempel 1963, Chambers & Leggett 1996, Chambers & Waiwood 1996, Marteinsdottir & Steinarsson 1998, Heyer et al. 2001). Fewer

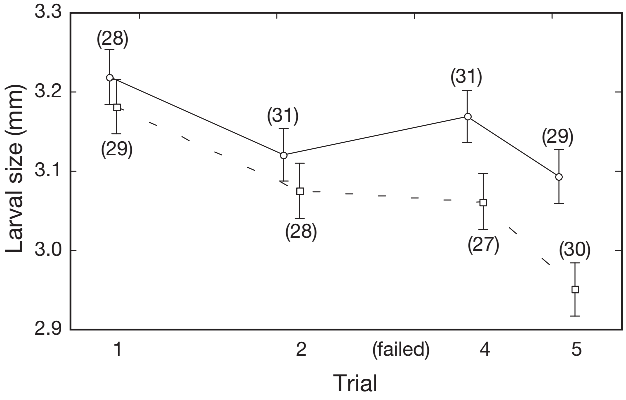

Fig. 3. *Symphodus roissali*. Larval size (±SE) over the reproductive period, excluding Trial 3. ——: averaged values for large females (>9 cm); – – – –: averaged values for small females (<9 cm); numbers in parentheses: sample size

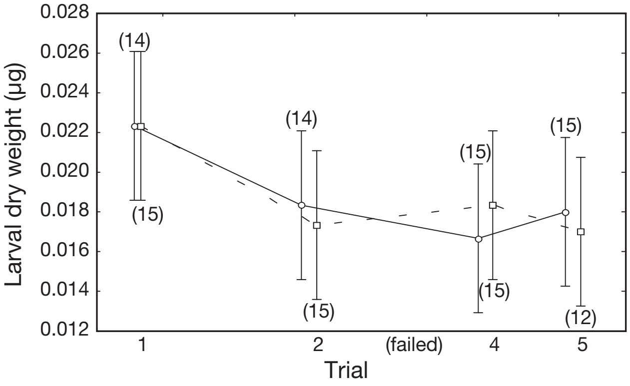

Fig. 4. *Symphodus roissali*. Larval dry weight (±SE) over the reproductive period, excluding Trial 3. ——: averaged values for large females (>9 cm); – – – –: averaged values for small females (<9 cm); numbers in parentheses: sample size

studies have reported the absence of a relationship between egg size and female size (Hinckley 1990, Wootton 1992, Trippel 1993) or a negative relationship (Broussard & Stickney 1981). In some cases, studies on the same species contradict one another with regards to this relationship (e.g. *Gadus morhua*: Kjesbu 1989 and Chambers & Waiwood 1996). For species showing a seasonal decline in egg size, an egg size–female size relationship may have been obscured in studies where this was not taken into account, which is also indicated by our results. Moreover, it is possible that time does not affect all female size classes in the same way. Large females produced larger eggs for a longer period of time than small females. However, the occurrence of a storm between the first 2 samplings could have affected small females more strongly than large ones: this could explain the observed decrease in egg size in the group of small females. However, testing this extreme would require an increased sampling effort.

The observed differences in egg mean diameter are also reflected in larval size. Throughout the spawning period, 'large' females produced significantly larger larvae than 'small' ones, and early in the season larvae were larger than late season. The results show that larger females can maintain their condition for a longer period over the spawning season and thus produce larger larvae for longer, whereas small females show a clear seasonal trend, producing smaller larvae as the reproductive period elapsed.

Egg and larval dry weights were not correlated with egg diameter and show different patterns. No differences can be attributable to female size, and only a decline in both parameters through spawning is apparent. As shown in previous studies (Rijnsdorp 1991, Kennedy et al. 2007), egg dry weight from individual females decreased as spawning progressed. The absence of a clear pattern among egg and larval dry weight remains unclear, and further studies are recommended.

Our observations of a positive relationship between some of the early life traits in fishes agree with most previous reports (Marteinsdottir & Steinarsson 1998, Heyer et al. 2001, and a review by Blaxter 1988). Large females produced larger eggs than small females, and larger larvae hatched from those eggs than from small eggs. Moreover, the relevance of our data lies in the fact that the difference between both classes of female size increases at the end of the reproductive period, suggesting that large females will be more effective during the overall spawning season. Larger larvae may have an advantage over smaller larvae in that they have been shown to swim faster and thus avoid predators more easily, search greater distances for food, find and capture larger sizes and quantities of prey, and survive longer periods of food shortages (Blaxter & Hempel 1963, Chambers et al. 1989, Chambers & Leggett 1996). These effects on mortality can have remarkable effects on post-recruitment processes (McCormick & Hoey 2004). This agrees with the statement of Houde (1987) that, in general, species with abbreviated larval stage durations have a high potential to regulate the year-class size at the juvenile stage.

Larval size is an important factor in the survival rate of *Symphodus roissali*, and juvenile survivors of this species showed larger sizes at hatching than settlers (Raventos & Macpherson 2005). Moreover, in the present study, we have found that larval size at hatching is affected by maternal size and time of spawning. Therefore, largest females of the population can have an important role in determining settlement and recruitment success.

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LITERATURE CITED

➤ Bergenius MAJ, Meekan MG, Robertson DR, McCormick MI (2002) Larval growth predicts the recruitment success of a coral reef fish. Oecologia 131:521–525

Bernardo J (1996) The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretation. Am Zool 36:216–236

Blaxter JHS (1988) Pattern and variety of development. In: Hoar WS, Randall DJ (eds) Fish physiology, Vol 3. Academic Press, New York, p 177–252

Blaxter JHS, Hempel G (1963) The influence of egg size on herring larvae (*Clupea harengus*). J Cons Int Explor Mer 28:105–114

➤ Broussard MC Jr, Stickney RR (1981) Evaluation of reproductive characters for four strains of channel catfish. Trans Am Fish Soc 110:502–506

Chambers RC (1997) Environmental influences on egg and propagule sizes in marine fishes. In: Chambers RC, Trippel EA (eds) Early life history and recruitment in fish populations. Chapman and Hall, New York, p 63–102

Chambers RC, Leggett WC (1996) Maternal influences on variation in egg sizes in temperate marine fishes. Am Zool 36:180–196

➤ Chambers RC, Waiwood KG (1996) Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua.* Can J Fish Aquat Sci 53:1986–2003

Chambers RC, Leggett WC, Brown JA (1989) Egg size, female effects, and the correlations between early life history traits of capelin, *Mallotus villosus*: an appraisal at the individual level. Fish Bull (Wash DC) 87:515–523

Einum S, Fleming A (2004) Environmental unpredictability and offspring size: conservative versus diversified bet-hedging. Evol Ecol Res 6:443–455

➤ García-Rubies A, Macpherson E (1995) Substrate use and temporal pattern of recruitment in juvenile fishes of the

Mediterranean littoral. Mar Biol 124:35–42

Green BS, McCormick MI (2005) Maternal and paternal effects determine size, growth and performance in larvae of a tropical reef fish. Mar Ecol Prog Ser 289:263–272

Green BS, Kenneth RN, McCormick MI (2006) Position of egg within a clutch is linked to size at hatching in a demersal tropical fish. J Exp Mar Biol Ecol 329:144–152

Hay DE (1985) Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Can J Fish Aquat Sci 42(Suppl 1): 111–126

Helas Th, Lejeune P, Michel Ch, Voss J (1982) A propos de quelques Poissons de la Méditerranée (suite) *Symphodus* (Crenilabrus) *roissali*, Risso, 1810. Rev Fr Aquariol 9: 29–32

Heyer CJ, Miller TJ, Binkowski FP, Calderone EM, Rice JA (2001) Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca fluvascens*). Can J Fish Aquat Sci 58:1477–1487

Hinckley S (1990) Variation of egg size of walleye pollock *Theragra chalcogramma* with a preliminary examination of the effect of egg size in larval size. Fish Bull (Wash DC) 88:471–483

Houde ED (1987) Fish early dynamics and recruitment variability. Am Fish Soc Symp 2:17–19

Houde ED (1994) Differences between marine and freshwater fish larvae: implications for recruitment. ICES J Mar Sci 51:91–97

Kamler E (1992) Early life history of fish: an energetics approach. Fish and Fisheries Series 4, Chapman and Hall, London

Kamler E (2005) Parent–egg–progeny relationships in teleost fishes: an energetics perspective. Rev Fish Biol Fish 15: 399–421

Kennedy J, Geffen AJ, Nash RDM (2007) Maternal influences on egg and larval characteristics of plaice (*Pleuronectes platessa* L.). J Sea Res 58:65–77

Kerrigan BA (1997) Variability in larval development of the tropical reef fish *Pomacentrus amboinensis* (Pomacentridae): the parental legacy. Mar Biol 127:395–402

Kjesbu OS (1989) The spawning activity of cod, *Gadus morhua* L. J Fish Biol 34:195–206

Koops MA, Hutchings JA, Adams BK (2003) Environmental predictability and the cost of imperfect information: influences on offspring size variability. Evol Ecol Res 5:29–42

Leis JM, Carson-Ewart BM (2001) Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. Coral Reefs 19:247–257

Lejeune P (1985) Le comportment sociaux des labrides mediterranéens. Cah Ethol Appl 5:1–208

Love RM (1980) The chemical biology of fishes: advances 1968–1977. Academic Press, New York

Marteinsdottir G, Steinarsson A (1998) Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. J Fish Biol 52:1241–1258

McCormick MI, Hoey AS (2004) Larval growth history determines juvenile growth and survival in a tropical marine fish. Oikos 106:225–242

Meekan M, Fortier L (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian shelf. Mar Ecol Prog Ser 137:25–37

Mills SC, Reynolds JD (2002) Mussel ventilation rates as proximate cue for host selection by bitterling, *Rhodeus sericeus*. Oecologia 131:473–478

Panagiotaki P, Geffen AJ (1992) Parental effects on size variation in fish larvae. J Fish Biol 41(Suppl B):37–42

Quignard DP, Pras A (1986) Labridae. In: Whitehead PJP, Bauchot ML, Hureau JC, Nielsen J, Tortonese E (eds) Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris, p 917–957

Raventos N (2004) Effects of wave action on nesting activity in the littoral five-spotted wrasse, *Symphodus roissali* (Labridae), in the northwestern Mediterranean Sea. Sci Mar 68:257–264

Raventos N, Macpherson E (2001) Planktonic larval duration and settlement marks on the otoliths of Mediterranean littoral fishes. Mar Biol 138:1115–1120

Raventos N, Macpherson E (2005) Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus.* Mar Ecol Prog Ser 285:205–211

Rijnsdorp AD (1991) Changes in fecundity of female North Sea plaice (*Pleuronectes platessa*) between three periods since 1900. ICES J Mar Sci 48:253–280

Sabatés A, Zabala M, Garcia-Rubies A (2003) Larval fish communities in the Medes Islands marine reserve (north-west Mediterranean). J Plankton Res 25:1035–1046

Shima JS, Findlay AM (2002) Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. Mar Ecol Prog Ser 235:303–309

Tamada K, Iwata K (2005) Intra-specific variations of egg size, clutch size and larval survival related to maternal size in amphidromus *Rhinogobious goby.* Environ Biol Fishes 73: 379–389

Tomkiewicz J, Morgan MJ, Burnett J, Saborido-Rey F (2003) Available information for estimating reproductive potential of Northwest Atlantic groundfish stocks. J Northwest Atl Fish Sci 33:55–70

Trippel EA (1993) Relations of fecundity, maturation, and body size of lake trout, and implications for management in northwestern Ontario lakes. N Am J Fish Manage 13: 64–72

Warner RR, Lejeune P (1985) Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. Mar Biol 87:89–99

Werner RG, Fuiman LA (2002) Methodological resources. In: Fuiman LA, Werner RG (eds) Fishery science: the unique contributions of early life stages. Blackwell Science, Oxford, p 289–300

Wootton RJ (1992) Constraints in the evolution of fish life histories. Neth J Zool 42:291–303

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