説参照)．現在では，東部，北部，および西部の多くの河川で，下流域にニジマスまたはブラウントラウト，上流域にはカワマス (Vincent and Miller, 1969; Gard and Flittner, 1974; Moore et al., 1983, 1986; Larson and Moore, 1985; Kozel and Hubert, 1989; Rahel and Hubert, 1991; Larsheid and Hubert, 1992)が生息し，中西部においてはさらに源流部にカットスロートトラウトが分布する (MacPhee, 1966; Griffith, 1972; Fausch, 1989; De Staso and Rahel, 1994)．これらの接触異所性分布の形成過程において，種間競争が重要な役割を果たしたことは，前節で述べた競争排除の研究例からも明らかである．しかし，ここで指摘したいのは，河川の源流域には移入種の侵入を拒んでいる在来種のカワマスもしくはカットスロートトラウトの単独生息域が残されているという事実である．北アメリカの移入種と在来種間および日本の在来種間にみられる接触異所性分布のメカニズムを理解するためには，種間競争の存在を証明するだけでは不十分なことは明らかである．すなわち，水温などの非生物学的要因が競争に代表される生物学的要因間の相互作用に与える影響の実体を明らかにすることが必要である (Fausch et al., 1994)．

条件特異型競争　近年，河川の流程に沿った物理的環境条件の勾配によって競争の帰結が変化する条件特異型競争が河川性サケ科魚類の分布域決定のメカニズムとして注目されている (De Staso and Rahel, 1994; Taniguchi et al., in preparation)．種間競争における優劣が特定の物理化学的環境下で逆転するという結果は，他の多くの生物群集で報告されている．例えば，動物プランクトン (Hessen et al., 1995)や両生類 (Warner et al., 1993)の種間ではpHが，またカダヤシ科魚類の種間においては塩分濃度が (Dunson and Travis, 1991)，競争の帰結をそれぞれ左右するという．また，水温と湿度がある種の甲虫 (Park, 1954)，水深が水性植物のガマ類 (Grace and Wetzel, 1981)における競争の帰結をそれぞれ逆転させることが知られている．淡水魚類の条件特異型競争に関する近年の研究では，水温の影響を扱ったものが多く見られ (Baltz et al., 1982; Persson, 1986)，特にサケ科魚類の種間およびサケ科魚類と同所的に生息する他の魚類との相互作用については，主に水温の調節が可能な室内の人工水路を用いた実験によって検討されてきている (Cunjak and Green, 1986; Glova, 1986; Reeves et al., 1987; De Staso and Rahel, 1994; ただし Symons, 1976参照)．

サケ科魚類異種個体間の干渉型競争における順位が水温環境によって逆転する場合があることは先に述べたが，さらに，この順位の変化に伴い競争個体の定位点の餌供給源からの距離や餌資源の消費量が逆転することも報告されている (De Staso and Rahel, 1994)．しかし，サケ科魚類と他の分類群の魚種の間では，必ずしも干渉型競争における順位の逆転といった単一の要因のみによって競争の帰結がもたらされるのではない．例えば，北アメリカ中西部の河川ではカワマス，ブラウントラウトおよびコイ科のクリークチャブの3種の分布域が上流から順に置き換わることが知られており (Rahel and Hubert, 1991)，この分布様式には種間競争が関与すると予想されている．これら3種間の競争系では，種間の優劣が水温傾斜によって逆転する過程が人工水路を用いた実験によって調査されている (Taniguchi et al., in preparation)．実験の結果，ブラウントラウトは中程度の広い水温範囲 (4–20°C)でカワマスより攻撃行動において優位であり，かつより多くの餌を消費したのに対し，低温(<4°C)ではこの順位関係が逆転しカワマスが優位となった．一方，これら2種とクリークチャブとの関係では，狭水温性のサケ科魚類が低，中程度 (<20°C)の水温下で攻撃行動によってクリークチャブを排除しより多くの餌資源の獲得に成功したのに対し，高水温下 (>20°C)では温度ストレスのためにサケ科魚類の干渉の機能と採餌能力が低下し，代わって高水温下における活動性の高いクリークチャブが最も多くの餌を消費するようになった．すなわち，これらのサケ科魚類種間では水温に依存して干渉型競争の影響が逆転するが，それらとクリークチャブとの競争では水温の上昇に従って影響の方向のみならずメカニズムが干渉型から資源消費型へと変化したと解釈される．また，Reeves et al. (1987)は，スチールヘッドトラウトとコイ科のレッドサイドシャイナー *Richardsonius balteaus* を用いた室内実験によって，水温に依存した競争メカニズムの変化を検討している．その結果によれば，低水温 (12–15°C)条件下ではスチールヘッドトラウトが干渉型競争において優位になり，よく成長したのに対し，高水温 (19–22°C)ではシャイナーはより機敏な採餌行動をとり，資源消費型競争において優位になる．これらの研究例は，少なくとも，異種個体間の競争の帰結には水温環境が強く関与することを証明するのに成功していると言える．

今後における研究の方向性

群集パターンの形成要因としての種間競争の重要性を検証する手段の一つとして，かつて，競争種の除去実験の有効性が強調された (Connell, 1983; Schoener, 1983)．確かに，競争関係が予測される多種系からある構成種を取り除いた後に，他の種の資源利用，採餌効率，成長量，そして特に個体数が変化すれば，この操作実験は少なくとも競争が存在することを示したことになる（除去実験の結果の解釈の問題点については伊藤ほか，1992参照）．しかしながら，ある条件下において競争の存在を証明できたとしても，競争の具体的なメカニズムが理解されなければ，群集パターンの予測は得られない．

近年，群集生態学の中心的な領域で扱われてきた諸問題は，群集を様々な機能集団や個体レベルに解体した上で個体群生態学や行動生態学などの手法を用いて再検討されるべきであると指摘されている (Price, 1986; Schoener, 1986b; Inchausti, 1994)．そして，生物群集中における競争関係を研究する際にはその存在自体の証明や帰結のみを問題にするのではなく，具体的なメカニズムの解明に主眼をおくべきであるとする提言がなされている (Price, 1986; Schoener, 1986b; Inchausti, 1994; Leibold, 1995)．このMechanistic approachと呼ばれる研究手法は，群集レベルで検出される現象を構成種の個体群の調節機構および行動，生理および形態などといった個体の属性についてのデータから説明しようとするものであり，従来の手法と比較して群集の構造や動態に関する定量的な予測性を得るのにより有効であると考えられている (Schoener, 1986b; Inchausti, 1994)．特に動物では，種数が少なく構造が比較的単純な群集においてすぐれた研究がなされてきており (Schluter and Grant, 1982; Spiller, 1984; Price, 1986)，淡水魚類においてもサンフィッシュ科魚類の3種間における資源分割メカニズムを最適採餌モデルを用いて明らかにしたWernerらの一連の研究 (Werner and Hall, 1976, 1977, 1979; Werner, 1984)を先駆的な例として挙げることができる．

先に述べたように，同所的に生息する複数種の淡水性サケ科魚類の異種個体間では，同種個体間の場合とほぼ同様な干渉行動が認められることが多く，この異種個体間干渉が種間の資源分割や競争排除と密接に関係していると考えられてきた (Fausch and White, 1986; Glova, 1986; Langeland et al., 1991)．しかしながら，この種間順位を個体レベルに解体した上で分析した研究は未だ少なく (Nakano and Furukawa-Tanaka, 1994; Nakano, 1995b)，多くの場合，種間における干渉競争の記載はA種からB種といった種レベルでの攻撃行動の方向性や相対的な頻度などに限られている (Griffith, 1972; Stein et al., 1972; Fausch and White, 1986; Glova, 1986)．そして，干渉行動の影響はその方向性と資源分割や競争排除の方向の一致性から推論的に導き出されることが多かったと言える．しかし一般的に，魚類は特異的な非限定成長 (Werner and Gilliam, 1984)を示すため陸上性の脊椎動物と比較して体サイズの種特性の制約が緩く，個体群のサイズ構造は同所的な近縁種間で著しく重複することが多い．異種間においても干渉型競争における優劣は通常体サイズによって決まるため，個体群の体サイズ構造が似かよった場合には競争能力も大きく重複すると予想される．したがって，一般に動物の種間競争は多くの場合非相称であり，個体群レベルでは一方のみが圧迫を受けることが多いという指摘とは異なり (Schoener, 1983)，魚類のような体サイズが重複する種間の干渉行動における優劣は個体レベルでは決して固定的なものではない．そのため，種を均質な競争能力を持った個体の集団として捉えて優位種・劣位種といった単純な対比を行うことは，むしろ種間競争の実体の把握を誤らせる恐れがある．

この異種個体間の干渉競争の解析は，先に述べてきた資源分割や競争排除の具体的なメカニズムを明らかにすると共に，その理論化を図る上で極めて重要である (Fig. 1)．例えば，ある種のニッチは様々な個体が占めるニッチの総和として表され (Roughgarden, 1972)，種のニッチシフトは個体群中のそれぞれの個体の採餌戦術や生息場所の利用様式の変化の平均値であると解釈することができる．魚類の採餌行動は可塑性が大きく，資源の分布や量，および個体の生理的な状況など様々な要因によって変化するが，中でも個体間の相互作用は最も重要な要因の一つである (Dill, 1983)．したがって，サケ科魚類にみられる異種個体間の干渉行動や環境変動が採餌行動に与える影響を行動生態学的な手法によって精細に解析し，さらには個体群レベルでの集積を図れば，資源分割に対する競争の影響についての個体を基軸とした理解が可能となるであろう．このようなアプローチによって，資源分割の程度や時間的な変異性に関するモデルをたて，それらの予測性を得ることができる

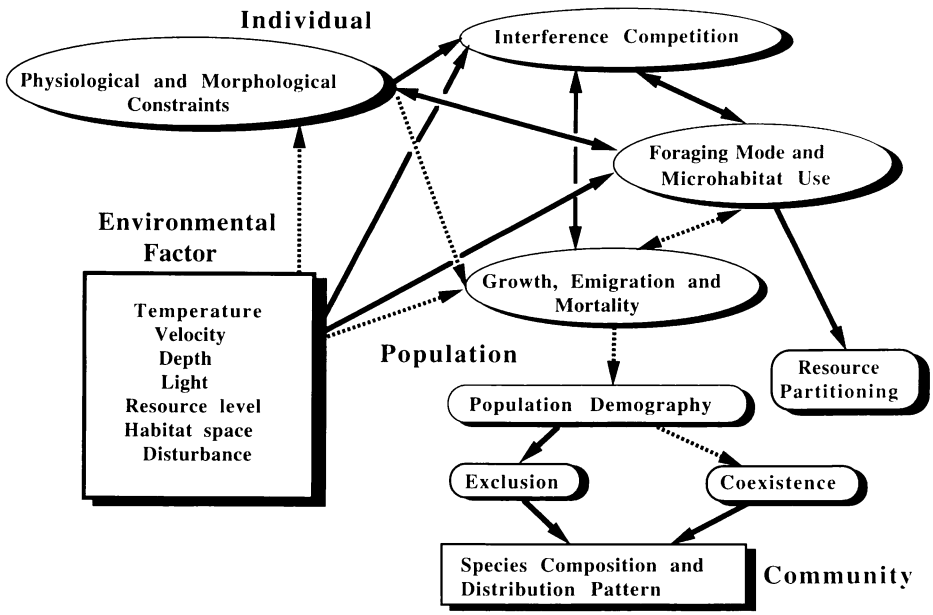

Fig. 1. Hierarchical schematization of competition mechanisms involved in freshwater salmonids systems, linking principal attributes within and between each level of organization. Solid arrows indicate the influence that were detected in the literatures reviewed. Dotted arrows show the potential pathways.

と考えられる．複数の研究者が指摘しているように (Schoener, 1986b)，この研究手法は構造が複雑な群集においてはデータが複雑になりすぎ現実的な手法とはなり得ないが，構造が比較的単純なサケ科魚類を主な構成要素とする群集においてはこの意味からも有効である．

一方，この資源分割によるサケ科魚類の競争種の共存，あるいは逆に競争排除および接触異所性分布などといった群集メカニズムの解明には，資源の利用様式に対する個体間の干渉の影響を明らかにするだけでは不十分であり，競争種双方の個体群のデモグラフィーに対する影響を明らかにする必要がある(Fig. 1)．自然条件下における河川性サケ科魚類の個体群サイズは，初期密度に拘わらず数年間にわたって一定のレベルに安定しており，生活史の比較的初期における密度依存的な移出率および死亡率の増大によって調節される場合が多い (Egglishaw and Shackley, 1977; Mortensen, 1977; Nakano and Nagoshi, 1985; Elliott, 1985, 1989, 1990)．この密度依存過程では，先に述べた個体間における干渉行動が直接的に関与すると考えられ (Chapman, 1962; Allen, 1969; McFadden, 1969; Nakano and Nagoshi, 1985)，特に干渉競争における劣位個体の分散が密度依存的な個体数調節において重要な役割を果たす考えられている (Chapman, 1962; Allen, 1969; Nakano, 1995a)．近年，Elliott (1990)およびGrant and Kramer (1990)は，密度依存的な個体群の調節過程が個体の成長に伴うなわばりサイズの拡大と非なわばり個体のハビタットからの移出によって説明できるとする一般仮説，すなわち「最大なわばりサイズ仮説」(Patterson, 1980の総説参照) を河川性サケ科魚類について再検討し，その有効性を示している．異種個体間における干渉競争 (種間順位および種間なわばり) は，種間において不足しがちな資源に対する要求の重複が大きく，かつ環境中における資源軸の時空間分化が乏しい場合には，種内のものと同様の機能を果たすと予想される (例えば，Fraser, 1969; Harvey and Nakamoto, 1996)．したがって，異種個体間における干渉型競争が各個体の資源利用のみならず成長，分散および死亡などに与える影響を明らかにすることによって，競争排除のメカニズムを明らかにできるものと思われる (Fig. 1)．

また，条件特異型競争のように競争の帰結が水温などの環境因子の影響で逆転する場合，特定の環境下では一方の種に競争に起因する個体の分散および死亡率の増大が起こり個体数が減少する可能性がある．したがって，環境因子によって個体

間の競争関係が逆転する生理的メカニズムと，さらには個体間の優劣の逆転が個体群の相互調節を介して個体群レベルでの排除の方向性を変化させることを明らかにすれば，接触異所性分布の形成に至るプロセスを説明することができるであろう．しかし，従来の研究ではこれら一連の過程が互いに独立したものとして捉えられたり，個体間の競争における優位種がすなわち群集の優占種となるなどといった結論付けが行われる場合もあり (De Staso and Rahel, 1994)，未だ個体間競争から個体群調節，そして環境傾斜に沿った接触異所性分布に至るプロセス全体を検討した研究例は皆無である．一方，このような干渉型競争の影響の方向性や強度に時間的な変動や比較的小さな空間規模での変異が認められる場合，さらには競争の影響自体が資源分割によって緩和される場合には，一方的な排除が起こらず長期的な共存が成立する場合もあると考えられる．しかし，淡水性サケ科魚類の異種共存機構を個体群の変動や調節過程を考慮して行われた研究は未だない．今後は，Chesson (1986)が指摘するように，物理的環境要因の影響を最も受けやすく，さらに個体数の調節が強く働く生活史初期における個体間相互作用と成長，分散，および生残などの個体群のデモグラフィーを考慮に入れた種間競争と異種共存機構の検討が強く望まれる．

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